BELEMNITES FROM THE CONIACIAN TO LOWER CAMPANIAN CHALKS OF NORFOLK AND SOUTHERN ENGLAND

by WALTER KEGEL CHRISTENSEN

ABSTRACT. Coniacian to Lower Campanian belemnite faunas from the chalks of Norfolk and southern England are described, using univariate and bivariate biometric analyses. The faunas include 13 species, subspecies and groups, referred to the following genera: *Actinocamax* Miller, *Gonioteuthis* Bayle, *Belemnellocamax* Naidin, and *Belemnitella* d'Orbigny. Two taxa, '*Actinocamax*' *lundgreni* Stolley and *Belemnitella p. propinqua* (Moberg) of the *Belemnitella* lineage, are new for England. The nominate subspecies of *Actinocamax verus* Miller and two other subspecies are discussed. Samples of *Gonioteuthis* Bayle are compared with samples of *Gonioteuthis* from NW Germany, Belgium and France, the biostratigraphy of which are well-known. The British specimens of *Belemnellocamax* ex gr. *grossouvrei* (Janet) are listed and reviewed. The concept of *B. praecursor* Stolley is discussed, as well as its relationship to the coeval *B. alpha* Naidin and to *B. mucronata* (Schlotheim) from the uppermost Lower Campanian and Upper Campanian. The localities are placed in the international stratigraphic framework on the basis of their belemnite faunas as well as other evidence. The traditional zonation of the Coniacian to Lower Campanian of the British Isles is tentatively correlated with the zonation of NW Germany. The German *Gonioteuthis* zonation of the upper Coniacian to Lower Campanian is critically assessed. The palaeobiogeography of the Upper Cretaceous belemnites of the North European Province is outlined, and the English Coniacian to Lower Campanian belemnite faunas are commented upon with respect to this framework.

SHARPE (1853) monographed the Upper Cretaceous cephalopods, including the belemnites, of the Chalk of England. In his work he described five belemnite species representing the genera *Neohibolites* Stolley, *Actinocamax* Miller, *Gonioteuthis* Bayle, and *Belemnitella* d'Orbigny. Almost a century later, Wright and Wright (1951) revised and commented briefly on the species described by Sharpe, as well as on species described by later authors. They listed 13 species which were referred to the following genera: *Neohibolites*, *Actinocamax*, *Gonioteuthis*, *Belemnocamax* Crick, *Belemnitella*, and *Belemnella* Nowak.

Since 1853 very little systematic palaeontology has been done on the Upper Cretaceous belemnites of Great Britain. This is surprising in view of the large amount of work done on English Lower Cretaceous belemnites and Cretaceous ammonites. As long ago as the 1930s, Brydone (1933, p. 287) stated that: 'Indeed there is hardly any more crying need than that for a thorough study of the belemnites of the Upper Chalk'.

Belemnites are uncommon in the Coniacian to Lower Campanian chalks of England. In the Upper Campanian and Maastrichtian they become more common. The belemnite faunas of the Coniacian to Lower Campanian include species of the *Gonioteuthis* lineage and *A. verus*, while species of the *Belemnitella* lineage occur sporadically and *Belemnellocamax* is very rare. The Upper Campanian belemnite faunas include only species of *Belemnitella*, and the Maastrichtian faunas comprise species of *Belemnella* with subordinate *Belemnitella*.

The scope of the present paper is to describe the belemnite faunas from the Coniacian–Lower Campanian chalks of Norfolk and southern England, utilizing biometric analysis. Southern England here includes Kent, Essex, Hampshire, and Wiltshire. The uppermost Lower Campanian belemnite fauna from southern England, consisting of *G. quadrata gracilis* (Stolley) and *B. mucronata* (Schlotheim), is not included in the present paper.

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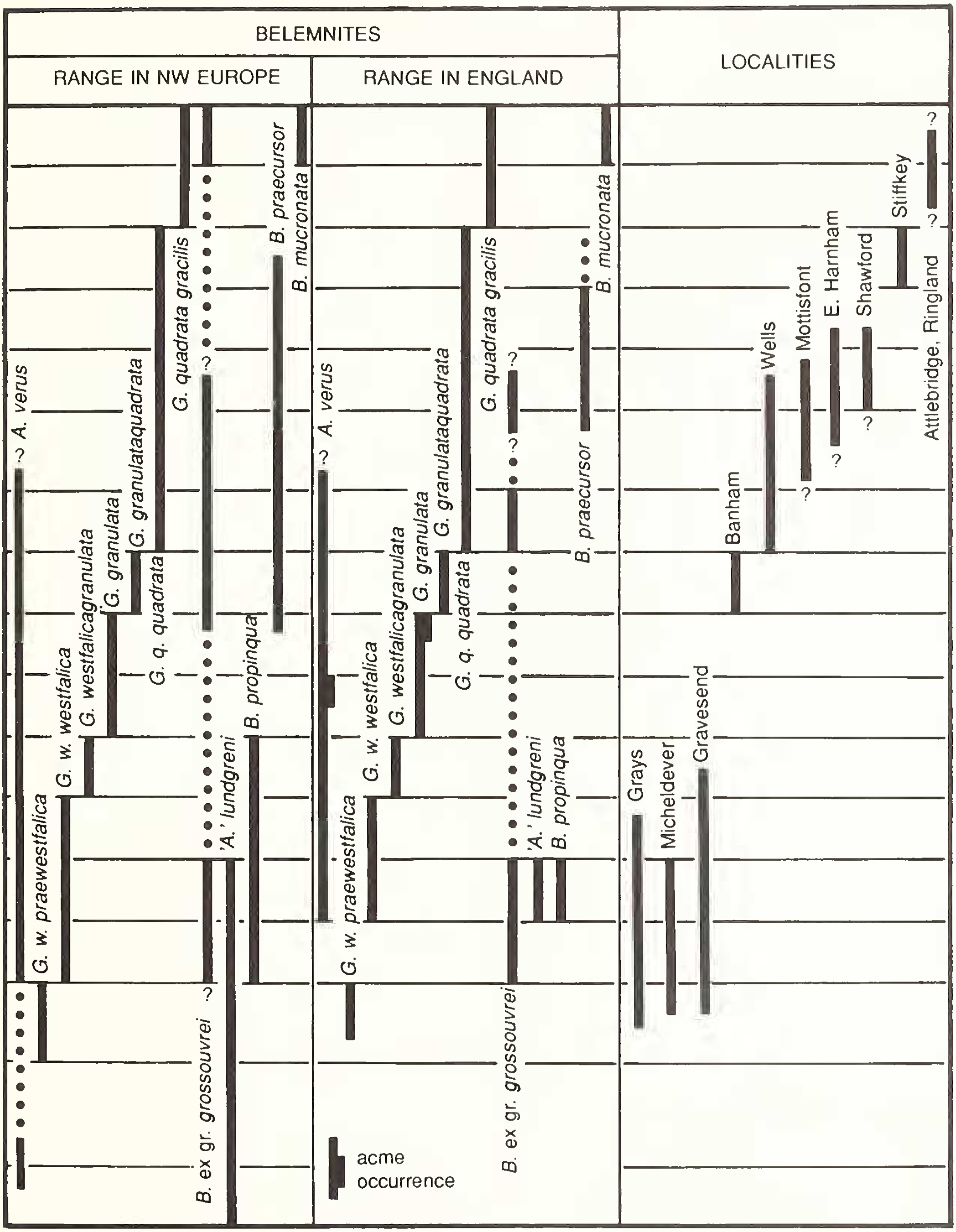
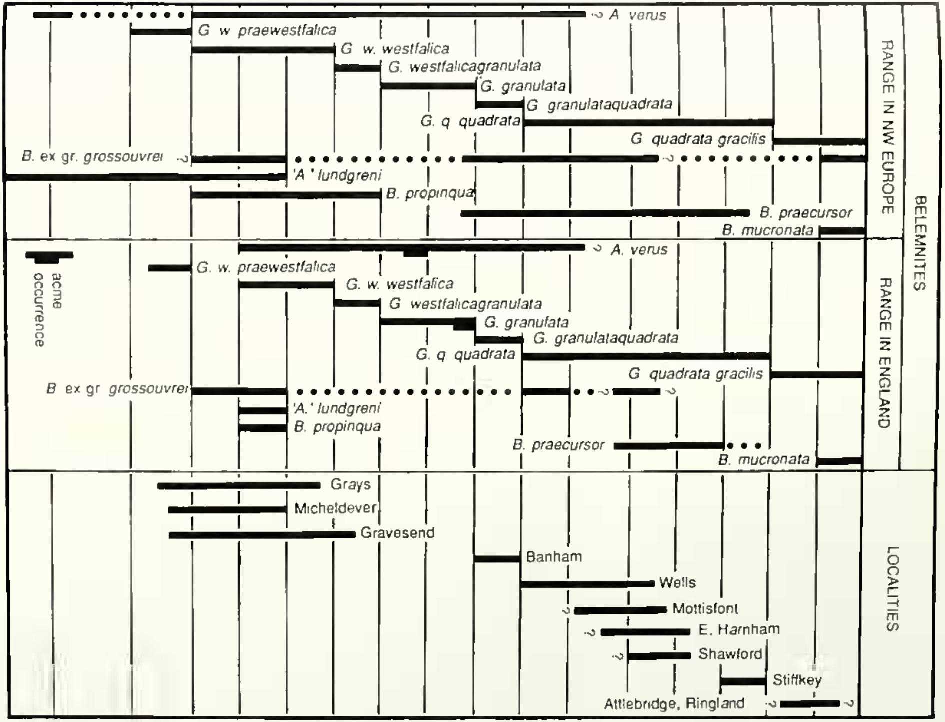
STAGE		ZONATION NW GERMANY	TRADITIONAL ZONES: SOUTHERN ENGLAND		TRADITIONAL ZONES: NORFOLK	STANDARD BELEMNITE ZONES NW EUROPE	
LOWER CAMPANIAN	upper part	*gracilis / mucronata* Zone	*Gonioteuthis quadrata* Zone	post-*Applinocrinus* beds	*Gonioteuthis* Zone (='Zone of granulated *Actinocamax*' sensu Brydone)	*G. quadrata gracilis / B. mucronata*	
		conica / gracilis Zone				*G. quadrata gracilis*	
		papillosa Zone		*Applinocrinus cretaceus* Subzone		*G. q. quadrata*	U
		senonensis Zone					
		pilula / senonensis Zone		*Hagenowia blackmorei* Horizon			
	lower part	*pilula* Zone	*Offaster pilula* Zone	Abundant *O. pilula* Subzone			
		lingua / quadrata Zone		*Echinocorys depressula* Subzone			L
		granulata-quadrata Zone				*G. granulataquadrata*	
SANTONIAN	U	*Marsupites / granulata* Zone	*Uintacrinus anglicus* Zone *Marsupites* Zone		*Marsupites* Zone	*G. granulata*	U
		Uintacrinus / granulata Zone	*Uintacrinus socialis* Zone		*Uintacrinus* Zone		L
	M	*rogalae / westfalica-granulata* Zone	*M. coranguinum* Zone		*M. coranguinum* Zone	*G. westfalica-granulata*	
		rogalae / westfalica Zone				*G. w. westfalica*	U
	L	*coranguinum / westfalica* Zone					L
		pachti / undulatoplicatus Zone					
CONIACIAN	U	*bucailli / praewestfalica* Zone				*G. westfalica praewestfalica*	
	M	*involutus / bucailli* Zone					
		koeneni Zone					
	L	*deformis* Zone	*M. decipiens* Zone *M. normanniae* Zone		*M. cortestudinarium* Zone		

TEXT-FIG. 1. Zonation and correlation of the Coniacian–Lower Campanian of NW Germany and England, standard belemnite zones in NW Europe, distribution of belemnites in NW Europe and England, and the age of localities according to the present study. The stratigraphical age of the localities is based on belemnites and other evidence.


BELEMNITES
RANGE IN NW EUROPE
RANGE IN ENGLAND
LOCALITIES
A. verus
G. w. praewestfalica
G. w. westfalica
G. westfalicagranulata
G. granulata
G. granulataquadrata
G. q. quadrata
G. quadrata gracilis
B. ex gr. grossouvrei
'A.' lundgreni
B. propinqua
B. praecursor
B. mucronata
acme occurrence
Grays
Micheldever
Gravesend
Banham
Wells
Mottisfont
E. Harnham
Shawford
Stiffkey
Attlebridge, Ringland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EARLIER WORK

In addition to Sharpe's monograph (1853), belemnites were described and figured by Miller (1823*a*, *b*), J. de C. Sowerby (1829), Blackmore (1896), Crick (1906, 1907, 1910), Sherborn (1906), and Brighton (1930). These papers, however, generally are characterized by descriptions of rare species. Jeletzky (1955*a*), in his paper on the evolution of Santonian and Campanian species of *Belemnitella*, also discussed and figured species of *Belemnitella* from the Campanian of England. Christensen (1974) made a morphometric analysis of *Actinocamax plenus* (Blainville) from the Plenus Marls of England, described *A. bohemicus* Stolley from the Middle Coniacian of Yorkshire (Christensen 1982), and discussed *A. primus* Arkhangelsky from England (Christensen 1990).

In addition to the papers mentioned above, English Upper Cretaceous belemnites were discussed, commented upon, and/or used biostratigraphically by Bailey *et al.* (1983*a*, 1984), Ernst (1966), Fletcher and Wood (1978, 1982) Jefferies (1961), Jeletzky (1951*a*, *b*), Peake and Hancock (1961, 1970), Reid (1971), Rowe (1901, 1904), Schulz (1979), and Wood (1967), to mention the most important papers.

MATERIAL

The belemnite material studied in the present paper was placed at my disposal by the Natural History Museum, London (BMNH), British Geological Survey, Keyworth, Nottingham (BGS), and Sedgwick Museum, Cambridge (SM). It consists of collections made during the last part of the nineteenth century and the beginning of the twentieth century, and includes the collections of H. P. Blackmore, A. W. Rowe, G. E. Dibley, and R. M. Brydone. In addition to these old collections, belemnites collected recently by C. J. Wood, P. Hammond, A. S. Gale and others are also included. The belemnites of the old collections are generally labelled only with locality name and zone. In contrast, the belemnites collected recently are very accurately horizoned with reference to lithological marker beds.

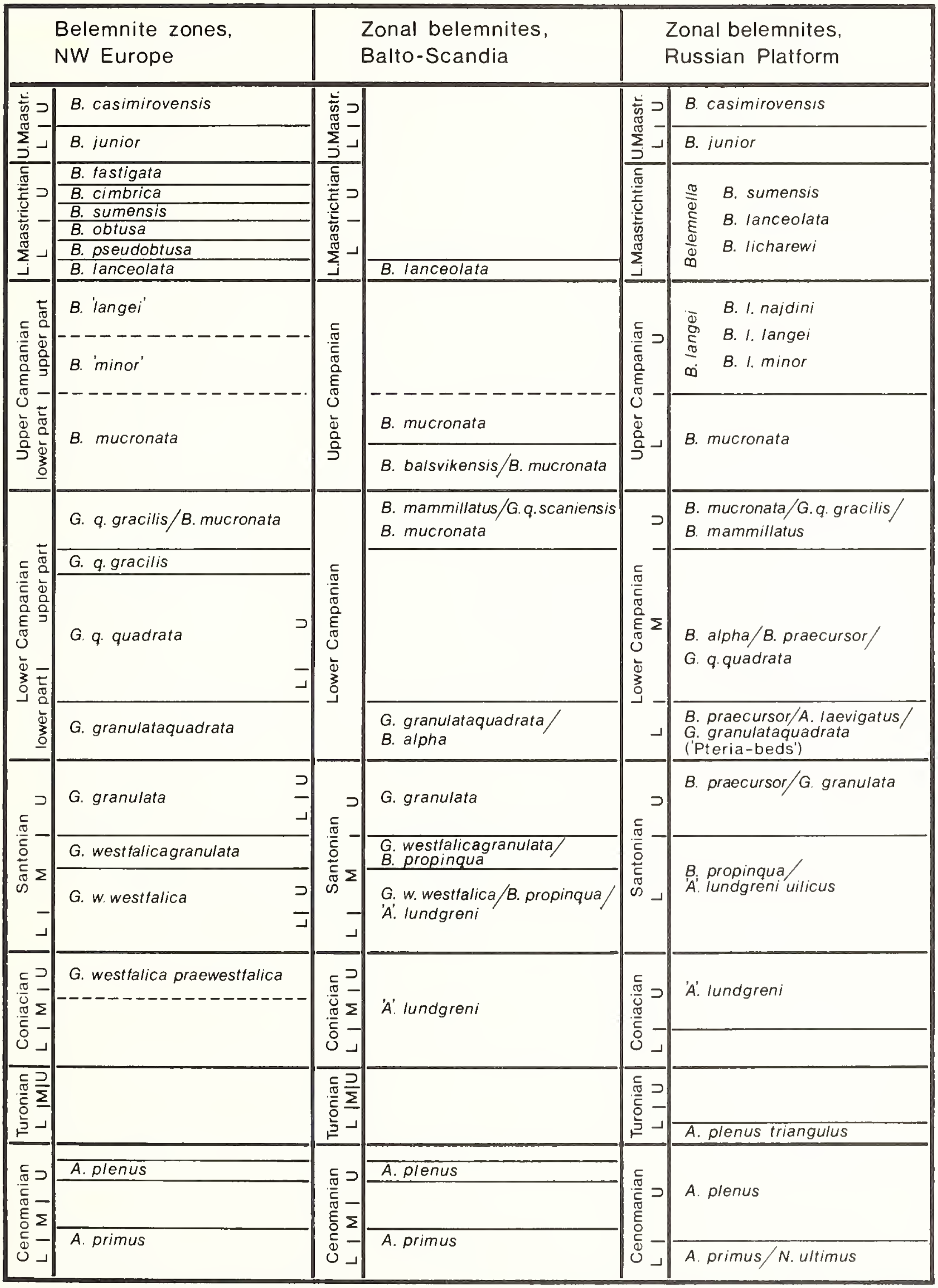
STRATIGRAPHY

The traditional zonation of the Coniacian–Maastrichtian of the British Isles was summarized by Hancock (1972) and Rawson *et al.* (1978) (cf. Text-fig. 1), and later discussed by, among others, Bailey *et al.* (1983*a*, *b*, 1984), Gale *et al.* (1987), Gale and Woodroof (1981), Mortimore (1986, 1987), Mortimore and Pomerol (1987), Pomerol *et al.* (1987), Robinson (1986, 1987), Stokes (1975, 1977), Wood (1981), and Wood and Mortimore (1988).

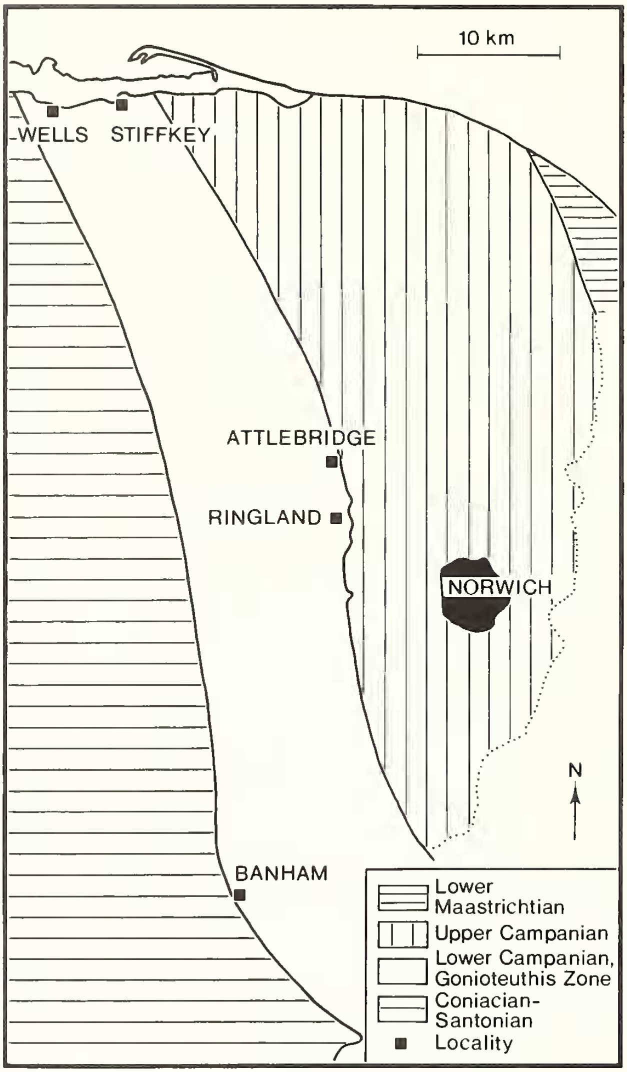
The Lower Campanian of southern England has been subdivided into several units (fossil horizons) (see Peake *in* Hancock 1972, table I, p. 114; see also Wood and Mortimore 1988); five of these units are shown in Text-figure 1. The Coniacian to Maastrichtian of Norfolk was studied by R. M. Brydone and A. W. Rowe at the beginning of the century; this work was summarized by Peake and Hancock (1961, 1970) and Wood (1988).

The Coniacian–Maastrichtian of NW Germany has been carefully studied during the last twenty-five years by a number of workers (see reviews by Ernst *et al.* 1979; Schulz *et al.* 1984). The zonation applied in Germany is used as a stratigraphic framework in the present paper.

The definition of the Coniacian–Lower Campanian chosen in the present paper is shown in Text-figure 1, and the belemnite zonations of NW Europe, Balto-Scandia, and the Russian Platform are shown in Text-figure 2. The correlation of the zonations in NW Germany and England is tentative and based mainly upon information presented by Bailey *et al.* (1983*a*, *b*, 1984). The *Uintacrinus socialis* Zone in England is defined by the first occurrence of its index fossil (Bailey *et al.* 1983*a*), whereas in Germany *U. socialis* occurs in both the *Uintacrinus/granulata* Zone and the upper part of the subjacent *westfalicagranulata* Zone (Ulbrich 1971; Ernst and Schulz 1974). The boundary between the Lower and Upper Campanian is placed at the extinction level of the genus *Gonioteuthis*. At the beginning of this century this boundary was placed at a lower level by British workers (e.g. Brydone 1912), namely at the first occurrence of *B. mucronata*. Fletcher and Wood (1978) suggested that the boundary as marked by the extinction level of *Gonioteuthis* was diachronous, being lower in Northern Ireland and England than in Germany.



TEXT-FIG. 2. Upper Cretaceous belemnite zones in western Europe, Balto-Scandia, and the Russian Platform (after Christensen 1988).



TEXT-FIG. 3. Map of Norfolk showing Lower Campanian *Gonioteuthis* Zone localities (modified from Peake and Hancock 1970).

LOCALITY DETAILS

The more important localities (Text-figs 3 and 4) mentioned in the text are listed below, with appropriate bibliographical information and National Grid References.

Norfolk (Text-fig. 3)
The chalk pits in the *Gonioteuthis* Zone of Norfolk were discussed by Peake and Hancock (1961, 1970) and Wood (1988).

Wells (TF 928429). According to Peake and Hancock (1970, p. 339A) this pit exposed about 40 m of chalk. The lowest beds were tentatively referred to the upper third of the *depressula* Subzone, the chalk in the middle of the quarry to the *cincta* belt of the Subzone of abundant *O. pilula*, and the top beds to the lowest third of the *H. blackmorei* Horizon.

The belemnites examined during the course of the present study were collected by P. Hammond. The entire section has yielded *Gonioteuthis*, but there is only sufficient material of *Gonioteuthis* for biometrical analysis from the lower third of the section. The specimens from this part of the section are referred to *G. q. quadrata* and are from the lower part of the *lingua/quadrata* Zone of the lower Lower Campanian. This part of the section also yielded *A. verus*. Moreover, I have seen a single specimen of *Belemnitella* sp., from the *pilula* Zone.

Stiffkey (TF 975428). The chalk pit was placed in the higher part of the *Gonioteuthis* Zone by Peake and Hancock (1970, p. 339A). The belemnites examined by me were collected by P. Hammond and include *G. q. quadrata* and *B.* cf. *praecursor*. The sample of *G. q. quadrata* is regarded to be from the upper Lower Campanian *papillosa* Zone.

Banham (TM 065878?). This is locality no. 129 of Rowe (MS and field notebooks preserved in the Palaeontology Library, BMNH, see Wood 1988). Peake and Hancock (1961, p. 313) recorded '... a typical *Echinocorys tectiformis* Brydone, such as would be expected from the lowest part of the *O. pilula* Zone;'. I have seen five specimens of *G. granulataquadrata* and three specimens of *A. verus* from Banham; the chalk of this pit is thus basal Campanian, *G. granulataquadrata* Zone.

Attlebridge (TG 134165). This is locality no. 168 of Rowe (MS and field notebooks, see Wood 1988). Peake and Hancock (1961) recorded several pits on Alderford Common, 1 mile north of Attlebridge. On the zonal map of Peake and Hancock (plate 1), Attlebridge is placed in the top of the *Gonioteuthis* Zone. I have seen a single specimen which may be referred to *G. quadrata gracilis*.

Ringland (TG 13951253). This is possibly locality no. 171 of Rowe (MS and field notebooks, see Wood 1988). According to Wood (1988) the pit is now overgrown and no chalk is visible. The pit was placed very high in the *Gonioteuthis* Zone by Wood (1988). I have seen a single specimen, which may be referred to *G. quadrata gracilis*.

Kent and Essex (Text-fig. 4)

Gravesend and Grays. The chalk pits of the Gravesend area, Kent, and the chalk pit at Grays, Essex, were mentioned briefly by Dibley (1900, 1918). He placed them in the top part of the *coranguinum* Zone. Dibley (1900) listed nine pits in the Gravesend area, including Fletcher and Co's Pit. Pits presently available expose chalk of latest Coniacian to Middle Santonian age (A. S. Gale pers. comm. 1985; C. J. Wood pers. comm. 1988).

The chalk pit at Grays has yielded the following belemnites: *G. w. westfalica*, *B. p. propinqua*, and '*A*'. ex gr. *lundgreni*. This belemnite fauna is Lower Santonian.

Belemnites from the Gravesend area include *G. w. westfalica*, *G. westfalicagranulata*, *B. p. propinqua*, '*A.*' *lundgreni*, *A. verus* and '*A.*' ex gr. *lundgreni*; these belemnites are from the upper Lower-Middle Santonian, Zones of *G. westfalica* and *G. westfalicagranulata*.

East Kent. The east Kent succession has yielded *G. westfalica praewestfalica*, *G. w. westfalica*, *G. westfalicagranulata*, *G. granulata*, and *A. verus*; *G. granulata* is common in the *Marsupites* Zone and *A. verus* in the *Uintacrinus* Zone (Bailey *et al.* 1983*a*).

I have studied three samples of *G. granulata* from east Kent (A. W. Rowe Colln, BMNH) (see below). They are said to come from the *Marsupites* Zone. On the basis of the mean Riedel Quotient, the sample from the Northdown brickworks pit near Margate can be assigned to the Upper Upper Santonian *Marsupites/granulata* Zone. The two samples from Rifle Butts and Margate, respectively, can be referred to the Lower Upper Santonian *Uintacrinus/granulata* Zone. This is at variance with the supposed age given on the labels and the discrepancy may be due to the small number of specimens in the two samples.

Hampshire (Text-fig. 4)
The chalk pits in Hampshire were listed by Griffith and Brydone (1911) and Brydone (1912).

Micheldever. This is locality no. 295 of Brydone (1912), which is a railway cutting north of the station (SU 518434). The cutting exposed chalk of *coranguinum* Zone age. The material in the Blackmore Colln, BMNH probably came from a working pit in the area, exposing chalk of the same age (A. S. Gale pers. comm. 1985). Micheldever has yielded *G. w. westfalica*, '*A.*' *lundgreni*, *B.* ex gr. *grossouvrei*, and *A. verus*. Moreover, several specimens of *Gonioteuthis*, which are destroyed at the alveolar end and therefore not determinable, are also known from this locality. These belemnites are Lower Santonian.

TEXT-FIG. 4. Map of eastern England showing localities and distribution of the Upper Cretaceous.

Shawford (SU 338274). This is locality no. 1086 of Brydone (1912), also known as Southampton Waterworks New Pit. This pit formerly exposed chalk of the lower *quadrata* Zone, possibly the *H. blackmorei* Horizon according to C. J. Wood (pers. comm. 1983) and A. S. Gale (pers. comm. 1985).

A small sample of *Gonioteuthis* from the 'lower course' sensu Brydone was analysed biometrically and compared with German samples of *Gonioteuthis*. The Shawford sample is referable to *G. q. quadrata* and is regarded to be from the middle Lower Campanian (see below).

I have also studied a small fauna of *Belemnitella* from this pit, mostly specimens without horizon details. The *Belemnitella* fauna is heterogeneous, in contrast to the *Belemnitella* fauna from East Harnham (see below), and includes *B.* cf. *praecursor* and *B. mucronata*. The *Belemnitella* specimens from the 'lower' or 'bottom course' are all *B.* cf. *praecursor*. *B. mucronata* appears in the uppermost Lower Campanian *mucronata/gracilis* Zone, and it thus seems that more zones were present at Shawford, spanning the middle to upper Lower Campanian. It is, however, possible that the specimens of *B. mucronata* came from another pit and were purchased from quarry workers.

Mottisfont (SU 337274). Brydone (1912) listed three pits situated north of the Mottisfont Station, locality nos 1065–1067, placed in the *quadrata* Zone. Brydone (1914) discussed locality no. 1067, also referred to as Mottisfont Whiting Pit, and he assigned the lower quarter to the Subzone of abundant *O. pilula*, whereas the upper three-quarters was assigned to the *quadrata* Zone.

Bailey *et al.* (1983*a*, p. 35) mentioned that the pit exposed chalk of basal *quadrata* Zone age, by and large equivalent to the *H. blackmorei* Horizon. According to Mortimore (1986, fig. 19), however, the pit showed chalks from the Old Nore Marl to above the Pepper Box Marls; the old Nore Marl is low in the Subzone of abundant *O. pilula* and the Pepper Box Marls are high in the *H. blackmorei* Horizon (Mortimore 1986, figs 20 and 22).

I have examined *B.* ex gr. *grossouvrei* and *A. verus* from Mottisfont. *A. verus* was also recorded by Brydone (1912) in addition to *G. quadrata*. The presence of *A. verus* is enigmatic, because this species is not recorded from above the *depressula* Subzone in southern England (see Bailey *et al.* 1983*a*, fig. 3; Mortimore 1986, fig. 20). In Germany, *A. verus* ranges up to the top of the *pilula* Zone *sensu germanico* at Misburg/Höver near Hannover (Ernst 1963*b*). The presence of *A. verus* at Mottisfont may therefore be explained in one of the following ways: (1) *A. verus* has a greater stratigraphic range than assumed by English workers, or (2) older beds may have been exposed formerly at Mottisfont.

Wiltshire (Text-fig. 4)

East Harnham (SU 140288). This pit on the south side of Salisbury is now backfilled, and the collections of Blackmore, now in BMNH, were probably mostly purchased from quarry workers (A. S. Gale pers. comm. 1985). The nearby section at West Harnham currently exposes high *pilula* Zone to basal *quadrata* Zone chalk, and it appears likely that East Harnham exposed approximately the same levels (A. S. Gale pers. comm. 1985).

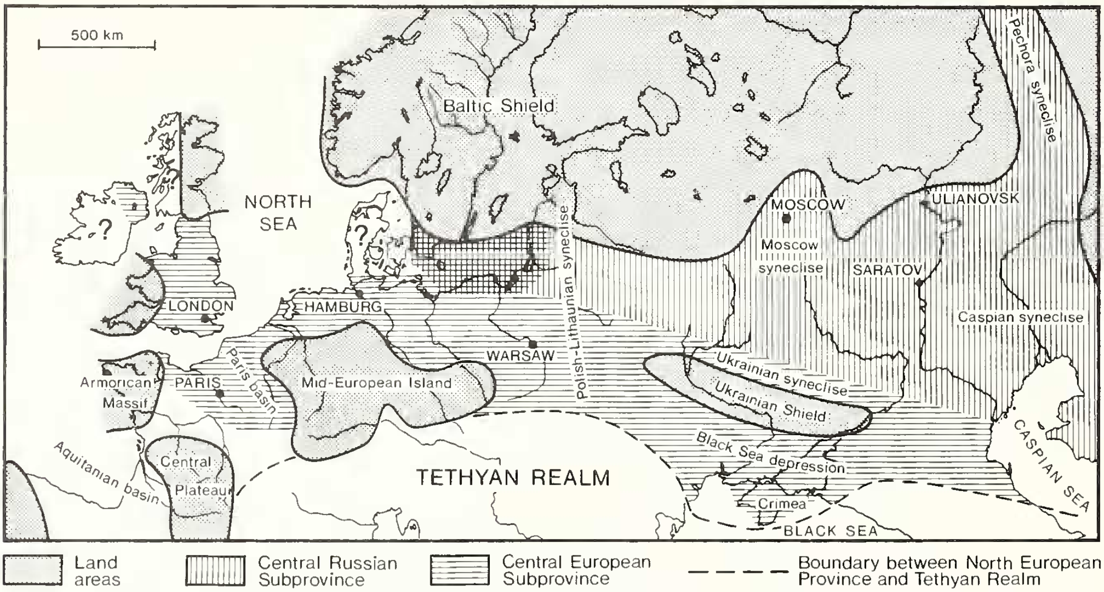
The belemnites from East Harnham include *G. q. quadrata*, *B. praecursor*, and *B.* ex gr. *grossouvrei*. The sample of *G. q. quadrata* is regarded to be from the middle Lower Campanian (see discussion below). According to Blackmore (1896), *B. lanceolata* (= *B. praecursor*) occurred in a thin band in the lower third of the *quadrata* Zone. The sample of *B. praecursor* is homogeneous in contrast to the *Belemnitella* fauna from Shawford (see above).

West Harnham. The only belemnite studied by me from this pit is the holotype of *Actinocamax blackmorei* Crick, which is referred to the *B. grossouvrei* group in the present paper. The chalk is presumed to be from the high *pilula* Zone-basal *quadrata* Zone (see above).

PALAEOBIOGEOGRAPHY OF THE UPPER CRETACEOUS BELEMNITES OF NW EUROPE

Christensen (1975*a*, 1976, 1982) surveyed the palaeobiogeography of the Upper Cretaceous belemnites of Europe (see also Combémorel *et al.* 1981), and consequently only a brief outline is given here. Belemnitellidae characterize the North Temperate Realm, but occur also in the northern part of the Tethyan Realm. They are unknown from the southern part of the Tethyan Realm and the South Temperate Realm.

The North Temperate Realm includes the North American and North European Provinces, and the latter comprises the Central European and Central Russian Subprovinces (Text-fig. 5). The subprovinces are well-defined in the Coniacian–Lower Campanian and characterized by independently evolving belemnite lineages: the *Gonioteuthis* lineage inhabited the Central European Subprovince and the *Belemnitella* lineage (including '*Actinocamax*' *lundgreni*) inhabited the Central Russian Subprovince. *A. verus* and *B.* ex gr. *grossouvrei* are widely distributed in both subprovinces; *A. verus* occurs commonly, while *B.* ex gr. *grossouvrei* is very rare (Christensen 1986).



TEXT-FIG. 5. Distribution of Upper Cretaceous biogeographic units in Europe based on belemnites. Upper Cretaceous land and sea areas represent maximum inundation for all stages. The boundaries are not reliable in detail, and the biogeographic units are typically gradational in character. After Christensen (1976).

After the extinction of the genera *Actinocamax* (in the middle Lower Campanian), *Gonioteuthis* (at the Lower–Upper Campanian boundary), and *Belemnellocamax* (in the lower Upper Campanian), the genus *Belemnitella* spread all over the North European Province in the Upper Campanian. The genus *Belemnella* appeared in the basal Maastrichtian and continued to the top of the Maastrichtian. In the Upper Campanian–Maastrichtian, however, no well-defined subprovinces can be recognized.

Norfolk and southern England are situated in the Central European Subprovince as defined by belemnites, but the genus *Gonioteuthis* is generally rarer here than elsewhere.

BELEMNITE FAUNAS OF THE UPPER CONIACIAN–LOWER CAMPANIAN

The late Coniacian chalk of east Kent has yielded a single specimen of *Gonioteuthis westfalica praewestfalica*.

The Lower–Middle Santonian belemnite faunas from Grays, Gravesend, and Micheldever consist of *G. w. westfalica*, *G. westfalicagranulata*, '*A.*' *lundgreni*, '*A.*' ex gr. *lundgreni*, *B. propinqua*, *A. verus*, and *B.* ex gr. *grossouvrei*. This diverse fauna includes taxa from both the Central European Subprovince (species of the *Gonioteuthis* lineage) and the Central Russian Subprovince (species of the *Belemnitella* lineage), in addition to the widespread *A. verus* and *B.* ex gr. *grossouvrei*. The species are very rare with one exception; *A. verus* occurs commonly at Gravesend. '*A.*' *lundgreni* has its main occurrence on the Russian Platform and in Balto-Scandia. Two specimens of '*A.*' *lundgreni* have been recorded earlier as *Gonioteuthis lundgreni*/aff. *westfalica* sensu Birkelund (see Ernst

1964*a*, pl. 3, figs 5 and 6) from the Münster Basin in NW Germany (Christensen 1973). *B. propinqua* has also its main occurrence on the Russian Platform and in Balto-Scania. Outside this area it has only been recorded from southern England (this paper). The specimens of '*A.*' *lundgreni*, '*A.*' ex gr. *lundgreni*, and *B. propinqua* from southern England may be regarded as stray specimens.

The Upper Santonian belemnite fauna consists of *G. granulata* and *A. verus*. According to earlier records, *G. granulata* is common in the *Marsupites* Zone and *A. verus* in the *Uintacrinus socialis* Zone.

The lower to middle Lower Campanian fauna includes *G. granulataquadrata* and *G. quadrata*, with subordinate *B. praecursor*, *B.* sp., *A. verus*, and *B.* ex gr. *grossouvrei*. This fauna includes taxa from both of the European subprovinces, as does the Lower to Middle Santonian fauna (see above). The specimens of *B.* cf. *praecursor* from Shawford, Stiffkey, and Porchester, as well as the specimens of *B.* sp. from Wells and the Sussex coast, may be regarded as stray specimens. *B. praecursor* occurred fairly commonly at East Harnham, and the population consists of all growth stages. This may indicate that *B. praecursor* lived and reproduced in that area during the middle Lower Campanian.

Fletcher and Wood (1978, pp. 93–94) suggested a *B. praecursor* event of considerable biostratigraphic significance in the lower part of the English *quadrata* Zone, by and large equivalent to the *Hagenowia* Horizon (= middle Lower Campanian). They believed that *B. praecursor* occurred at this stratigraphic level in Northern Ireland, Shawford in Hampshire, Bramford and Claydon near Ipswich in Suffolk, Stiffkey in Norfolk, and Hallembaye in eastern Belgium.

In Scania, NW Germany, and Belgium, the genera *Gonioteuthis* and *Belemnitella* occur together in the basal Lower Campanian: *G. granulataquadrata* and *B. alpha* in Scania (Christensen 1975*a*, 1986), *G. granulataquadrata* and *B. praecursor* at Braunschweig (Ernst 1964*b*, 1968), *G. quadrata* and *B. alpha*, *B.* aff. *mucronata/praecursor* or *B.* aff. *senior/praecursor* in the Münster Basin in NW Germany (Ernst 1964*b*, Christensen 1986), and *G. quadrata* and *B. praecursor* at Hallembaye in Belgium (Christensen and Schmid 1987). In Scania and NW Germany, the basal Lower Campanian *Gonioteuthis/Belemnitella* assemblage also includes *B.* ex gr. *grossouvrei* and *A. verus*. As shown above, *B. praecursor* from East Harnham and *B.* cf. *praecursor* from Shawford are from the middle Lower Campanian, whereas *B.* cf. *praecursor* from Stiffkey is from the *papillosa* Zone of the upper Lower Campanian. I have briefly studied a sample of *Belemnitella* sp., consisting of more than 100 specimens, from Bramford. This sample was collected by R. M. Brydone and is housed in the Ipswich Museum. On the basis of the external characters only, this sample seems to be more advanced than the samples of *B. praecursor* from Hallembaye and East Harnham, and it may have come from a higher part of the Lower Campanian. In the Corbières area of the French Pyrenees, *B. praecursor* has recently been recorded from the uppermost Santonian (Christensen *et al.* 1991).

It can thus be concluded that there is no evidence for a *Belemnitella praecursor* event in the middle Lower Campanian as suggested by Fletcher and Wood (1978), even if *B. praecursor* is recorded from the middle Lower Campanian of Northern Ireland and southern England.

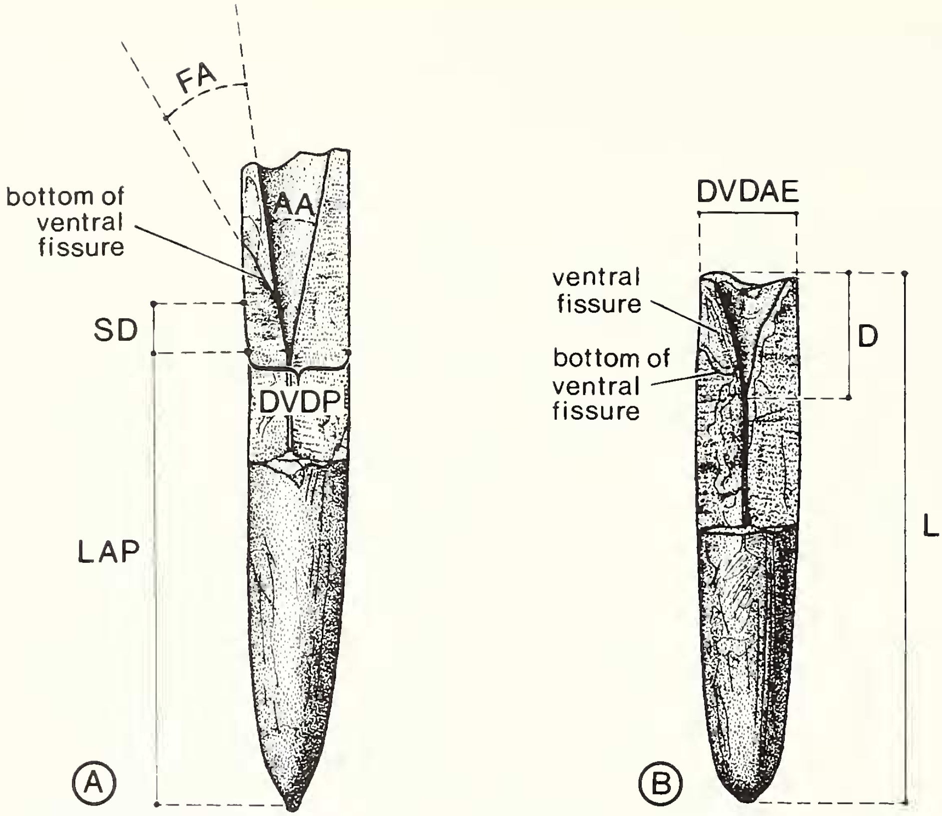
SYSTEMATIC PALAEONTOLOGY

Morphology of the guard and terminology. The guard is usually the only part of the skeleton preserved, and both external and internal characters are used for taxonomic classification.

The following characters are generally considered to be of taxonomic value in describing Upper Cretaceous belemnites belonging to the Belemnitellidae Pavlow: (1) size of guard; (2) shape of guard; (3) structure of the anterior end; (4) surface markings; (5) internal characters; and (6) ontogeny. The characters were discussed recently by Christensen (1986).

The Riedel Quotient (Ernst 1964*a*) is the ratio of length of guard divided by depth of pseudoalveolus, and the Schlankheits Quotient (= Slenderness Quotient) of Ernst (1964*a*) is the ratio of length of guard divided by dorso-ventral diameter at the anterior end.

Measurements and abbreviations. A list of measured characters and abbreviations is given below (cf. Text-fig. 6): total length of guard (L), length from apex to protoconch (LAP), dorso-ventral diameter at protoconch



TEXT-FIG. 6. Diagram showing the morphological elements of the guard in (A) *Belemnitella praecursor* and (B) *Gonioteuthis quadrata*. L = length of the guard; LAP = length from the apex to the protoconch; D = depth of the pseudoalveolus; SD = Schatzky distance; DVDP = dorso-ventral diameter at the protoconch; DVDAE = dorso-ventral diameter at the alveolar end; FA = fissure angle; and AA = alveolar angle. After Christensen and Schmid (1987).

(DVDP), lateral diameter at protoconch (LP), dorso-ventral diameter at alveolar end (DVDAE), lateral diameter at alveolar end (LDAE), maximum lateral diameter (MLD), Schatzky distance (SD), alveolar angle (AA), fissure angle (FA), Riedel Quotient (RQ), and Slenderness Quotient (SQ).

Linear measurements were made with a vernier caliper to an accuracy of 0·1 mm, and angles were measured with a goniometer ocular fitted on a WILD stereomicroscope to an accuracy of 0·5°.

Biometric methods. Species and subspecies variability is analysed using univariate and bivariate statistical methods and is summarized by descriptive statistics, histograms, and scatter diagrams. The statistics were calculated according to standard formulae presented by Simpson *et al.* (1960) and Sokal and Rohlf (1969). The statistical methods and tests used in the present paper were discussed at length by Christensen (1975*a*, pp. 31–33).

In the univariate analyses estimates of the following statistics were calculated: arithmetical mean value ($\bar{X}$), standard deviation (SD), and coefficient of variation (CV). In addition, observed range (OR) is reported, and N is the number of specimens.

The regression line is written: $y = a+bx$, and the original measurements were used in the calculations, because of the linear trend on ordinary graph paper and the homoscedastic variance around the regression line. Estimates of the following statistical parameters were calculated: the slope (b) and standard deviation of the slope (SD_b); the intercept on the y-axis (a) and the standard deviation of the intercept (SD_a); the variance (SD^2_{yx}) and the standard deviation (SD_{yx}) of the regression line; and the correlation coefficient (r). N is the number of specimens. The correlation coefficients were tested for significance by using table Y in Rohlf and Sokal (1969), and *t*-tests on the *y*-intercepts were performed in order to see if the intercept differed significantly from zero. The regression lines of two samples were compared in the way described by Hald (1957, pp. 571–579).

I have earlier discussed the disadvantages of using ratios in palaeontological studies (Christensen 1973, 1974, 1975*a*, 1988) especially in cases where growth is allometric. In the present paper, various ratios were calculated only in order to facilitate comparison with samples of belemnites described by earlier authors.

Order BELEMNITIDA Zittel, 1895
Suborder BELEMNOPSEINA Jeletzky, 1965
Family BELEMNITELLIDAE Pavlow, 1914

Type genus. Belemnitella d'Orbigny, 1840.

Diagnosis. See Christensen (1975*a*).

Distribution. Belemnitellidae are restricted to the Upper Cretaceous and are reported from the Lower Cenomanian to the Upper Maastrichtian. They are mainly distributed in the North Temperate Realm. A few representatives are also recorded from the northern part of the Tethyan Realm.

Genus ACTINOCAMAX Miller, 1823

Type species. Actinocamax verus Miller, 1823 by original designation.

Remarks. Naidin (1964) recognized three subgenera within *Actinocamax*: *A*. (*Actinocamax*), type species *A. verus* Miller, 1823; *A*. (*Praeactinocamax*), type species *A. plenus* (Blainville, 1825); and *A*. (*Paractinocamax*), type species *A. grossouvrei* Janet, 1891. This classification was discussed by Christensen (1982, 1986) and is not followed here. Species belonging to *A*. (*Actinocamax*) and *A*. (*Praeactinocamax*) differ only in size, and species referred to *A*. (*Paractinocamax*) by Naidin are placed in the genus *Belemnellocamax* Naidin (see discussion below).

Distribution. Actinocamax ranges from the Lower Cenomanian to the middle Lower Campanian. It is distributed in the North European and North American Provinces.

Actinocamax verus Miller, 1823

Plate 1, figs 1–9

1823*b* *Actinocamax verus* Miller, p. 64, pl. 9, figs 17 and 18 (non pl. 3, figs 16–20).
1906 *Actinocamax verus* Miller; Sherborn, p. 152, pl. 15, figs 4 and 5.
1952 *Actinocamax verus* var. *duestrensis* Naidin, p. 66, pl. 1, fig. 9; pl. 2, figs 1 and 2.
1962 *Actinocamax verus duestrensis* Naidin; Kongiel, p. 113, pl. 20, figs 14–17.
1964 *Actinocamax* (*Actinocamax*) *verus verus* Miller; Naidin, p. 28, text-figs 9 and 10, 18.
1964 *Actinocamax* (*Actinocamax*) *verus duestrensis* Naidin; Naidin, p. 29.

Type. Lectotype, here designated, the original of Miller (1823*b*, pl. 9, figs 17 and 18).

Material. More than two hundred specimens in the BMNH, BGS, and SM collections: about one hundred specimens from the *coranguinum* Zone of Gravesend, Kent (e.g. Red Lion Pit and Fletcher's Pit) and Micheldever, Hampshire (including BMNH C42708–99 and SM B836–9 from Gravesend, BMNH C43367–77, C44167 and SM B100082–3 from Micheldever); about one hundred specimens from the *Uintacrinus socialis* Zone of southern England (including BMNH C43393–486, SM B65905–19, BGS Zt848); and about one dozen specimens from the *pilula* and *quadrata* Zones of southern England and the *Gonioteuthis* Zone of Norfolk (including BMNH C43357–8, BMNH C44876, BMNH C43359–61, BGS GSM 101426).

Description. An *Actinocamax* with a small, stout guard which is lanceolate in lateral and ventral views. The guard is flattened ventrally and the anterior end is compressed. The anterior end may have a low or high cone-shaped alveolar fracture, be flat, or even have a shallow pseudoalveolus. There is a small pit in the anterior end for housing the posterior part of the phragmocone. The alveolar fracture is symmetric or asymmetric, and in the latter case the dorsal side is more incised than the ventral side. The alveolar fracture may be sharply demarcated from the surface of the guard or may continue gradually into the surface of the guard. The anterior end exhibits concentric growth layers of the guard and radiating ribs. Dorso-lateral longitudinal depressions are faintly developed, and the vascular imprints are weakly developed or not present. The ventral fissure and ventral furrow are not preserved. The surface of the guard may be covered by granules which may form corrugated transverse lines.

Remarks. A. verus can be distinguished easily from other species of *Actinocamax* by its small size and stout guard. Specimens of *A. verus* having a flat anterior end or a shallow pseudoalveolus differ from juvenile specimens of *G. westfalica* in being stouter and more lanceolate in ventral view. Naidin (1964) recognized three subspecies of *A. verus*: *A. v. verus*, *A. verus fragilis* Arkhangelsky, and *A. verus dnestrensis* Naidin, mainly on the basis of the structure of the anterior end. The subspecies were discussed by Christensen (1986), who placed *A. verus dnestrensis* in synonymy with *A. v. verus*, and suggested that *A. verus fragilis* may be considered as a geographic subspecies prevailing on the Russian Platform.

Two samples of *A. verus*, one from the Red Lion Pit, Gravesend (basal Santonian) (BMNH C42708–99), and another from Margate, Kent (Lower Upper Santonian) (BMNH C43393–486), were analysed with respect to the structure of the anterior end (Table 1). In addition, the analysis of two samples of *A. verus* from Scania, Sweden is also reported (Christensen 1986).

All samples showed a series of forms ranging from specimens with a high cone-shaped alveolar fracture (*fragilis*-like specimens), through specimens with a low cone-shaped alveolar fracture (*verus*-like specimens), to specimens with a shallow pseudoalveolus (*dnestrensis*-like specimens), with all intermediate forms. The specimens of the four samples, nevertheless, were subdivided into three groups, although it was difficult in some cases to decide to which group an individual specimen should be assigned. Most specimens in all four samples belong to group 1 (Table 1). A few specimens belong to groups 2 and 3. In the opinion of the author the samples exhibit a normal variation with respect to the structure of the anterior end; similar variations are also seen in other

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EXPLANATION OF PLATE 1

Figs 1–9. *Actinocamax verus* Miller. 1–3, BGS GSM 101427, great cutting north of Micheldever, locality 295 of Brydone (1912), *coranguinum* Zone; 1, dorsal view; 2, lateral view; 3, view of the anterior end, ×2. 4–6, BGS GSM 101426, Mottisfont, locality 1067 of Brydone (1912), *quadrata* Zone; 4, dorsal view; 5, lateral view; 6, view of the anterior end, ×2. 7–9, BGS Zt848, Grenham Bay, Birchington, Kent; uppermost 2 m of *U. socialis* Zone. 7, dorsal view; 8, lateral view; 9, view of anterior end, ×2.

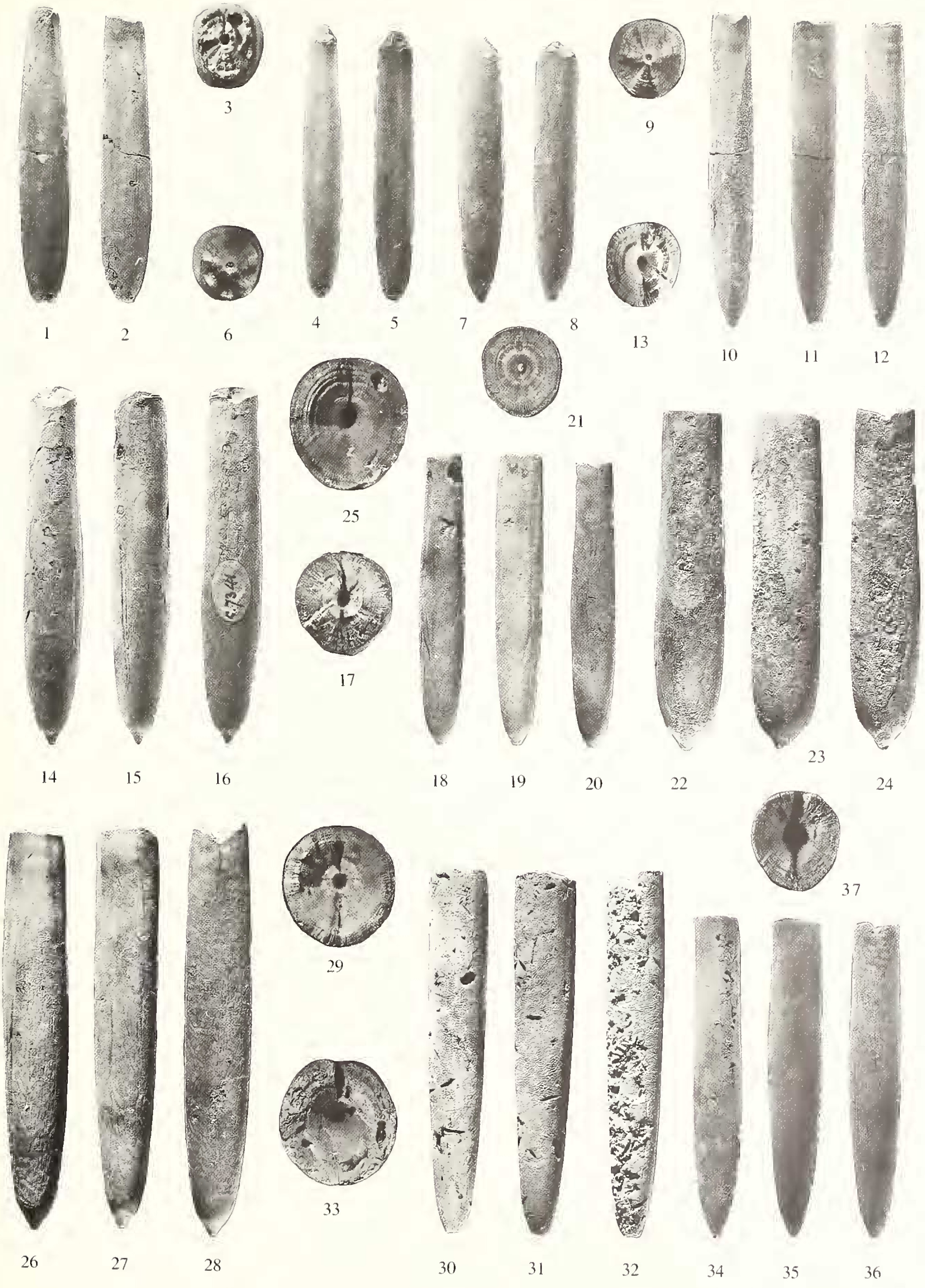
Figs 10–13. *Gonioteuthis westfalica praewestfalica* Ernst and Schulz, BGS GSM 118339, West Cliff, Ramsgate, Kent; *coranguinum* Zone, 10·0–10·5 m beneath Bedwell's Columnar Band; 10, dorsal view; 11, lateral view; 12, ventral view; 13, view of the anterior end, ×2.

Figs 14–29. *Gonioteuthis westfalica westfalica* (Schlüter). 14–17, BMNH C7341, Grays, Essex, *coranguinum* Zone; 14, dorsal view; 15, lateral view; 16, ventral view; 17, view of the anterior end, ×2. 18–21, BMNH C44381, Micheldever, *coranguinum* Zone; 18, dorsal view; 19, lateral view; 20, ventral view; 21, view of the anterior end, ×2. 22–25, BMNH C43497, Gravesend, *coranguinum* Zone; a short and stout specimen; 22, dorsal view; 23, lateral view; 24, ventral view; 25, view of the anterior end, ×2. 26–29, BMNH C43496, Gravesend, *coranguinum* Zone; 26, dorsal view; 27, lateral view; 28, ventral view; 29, view of the anterior end, ×2.

Figs 30–37. *Gonioteuthis westfalicagranulata* (Stolley). 30–33, BMNH C43521, Gravesend, *coranguinum* Zone; 30, dorsal view; 31, lateral view; 32, ventral view; 33, view of the anterior end, ×2. 34–37, BGS Zt1960, White Ness near Kingsgate, Kent, *coranguinum* Zone, 1 m above Barrois Sponge Bed; 34, dorsal view; 35, lateral view; 36, ventral view; 37, view of the anterior end, ×2.

All specimens are coated with ammonium chloride and the figures are natural size unless otherwise stated.

PLATE 1



CHRISTENSEN, *Actinocamax*, *Gonioteuthis* samples of *Actinocamax*, i.a. *A. plenus* (see Christensen 1974), and in *G. westfalica* (see Ernst 1964*a*; Christensen 1975*a*). It should, however, be stressed that there is apparently an increase in the number of *fragilis*-like specimens from the basal Santonian to the basal Campanian. Ernst (1964*b*, p. 181) has also reported that *fragilis*-like specimens are more common in the basal Campanian than in the basal Santonian. This apparent trend in the development of the structure of the anterior end may be real, but should be tested by further studies.

Locality	Age	Group 1	Group 2	Group 3	Σ
Kullemölla, Scania	basal Campanian	122 (79%)	26 (17%)	6 (4%)	154
Margate, Kent	Lower Upper Santonian	61 (77%)	16 (20%)	2 (3%)	79
Eriksdal, Scania	upper Middle Santonian	100 (86%)	9 (8%)	7 (6%)	116
Red Lion Pit, Gravesend	basal Santonian	80 (94%)	1 (1%)	4 (5%)	85

TABLE 1. Estimates of relative abundance of three groups of *Actinocamax verus*. Group 1 contains specimens with a low cone-shaped alveolar fracture (*verus*-like specimens); group 2 includes specimens with a high cone-shaped alveolar fracture (*fragilis*-like specimens); and group 3 contains specimens with a shallow pseudoalveolus (*dnestrensis*-like specimens).

Distribution. A. verus is widespread in the North European Province. In NW Europe it is recorded mainly from the uppermost part of the Lower Santonian *I. undulatoplicatus* Zone to the middle Lower Campanian *Offaster pilula* Zone *sensu germanico*. In off-shore chalks *A. verus* is most common in the Upper Santonian. *A. verus* is also known from the Lower to Middle Coniacian of Bornholm, Denmark (personal observation). On the Russian Platform it occurs in the Turonian to lower Lower Campanian (Naidin 1964).

Genus GONIOTEUTHIS Bayle, 1878

Type species. Belemnites quadratus Blainville, 1827 by original designation.

Remarks. The evolutionary lineage of *Gonioteuthis* (in ascending order): *G. westfalica praewestfalica* Ernst and Schulz, *G. w. westfalica* (Schlüter), *G. westfalicagranulata* (Stolley), *G. granulata* (Blainville), *G. granulataquadrata* (Stolley), *G. quadrata quadrata* (Blainville), and *G. quadrata gracilis* (Stolley), has been studied especially by Stolley (1897, 1916, 1930), Ernst (1963*a*, *b*, 1964*a*, *b*, 1966, 1968), Ernst and Schulz (1974), Christensen (1975*a*, *b*, 1986, 1988), Christensen and Schmid (1987), and Jarvis (1980).

Naidin (1964) recognized two subgenera of *Gonioteuthis*: *G.* (*Gonioteuthis*), type species *Gonioteuthis quadrata* (Blainville); and *G.* (*Goniocamax*) Naidin, type species *Actinocamax lundgreni* Stolley. The subgenera were treated later as genera by, among others, Naidin and Kopaevich (1977) and Naidin (1981). Naidin (1964) placed the earliest members of the *Gonioteuthis* lineage in the subgenus *Goniocamax*, in addition to '*Actinocamax*' *lundgreni* Stolley, and other species from the Russian Platform, Greenland, and North America. The classification of Naidin was discussed by Ernst and Schulz (1974) and Christensen (1982, 1986) and is not followed here. '*A.*' *lundgreni* and *G.* (*Goniocamax*) are discussed further below.

The *Gonioteuthis* lineage provides a good tool for biostratigraphy. It is, however, necessary to analyse homogeneous samples of a certain size in order to make a reliable specific determination, and limited material has little stratigraphic value (Ernst 1964*a*; Christensen 1975*a*) (see also below). Only the earliest member of the lineage, *G. westfalica*, is easily recognizable owing to its structure of the anterior end.

Ernst (1963*a*, *b*, 1964*a*, *b*, 1966, 1968) and Ernst and Schulz (1974) characterized samples of *Gonioteuthis* on the basis of the mean values of various ratios, including the Riedel Quotient and the Slenderness Quotient (Schlankheits Quotient of Ernst).

In order to analyse the growth relationship of various characters, I have calculated regression lines by the least squares method of samples of *Gonioteuthis* from NW Germany on the basis of Ernst's original measurements, which he kindly placed at my disposal. In addition, samples from Sweden, Bornholm (Denmark), Belgium, France, and England have also been analysed (Christensen 1971, 1973, 1975*a*, *b*, 1986, herein; Christensen and Schmid 1987).

1. *Length of guard* vs *depth of pseudoalveolus*. 24 samples of *Gonioteuthis* were analysed, including 3 samples of *G. westfalica* from NW Germany and Bornholm, 3 samples of *G. westfalicagranulata* from NW Germany and Sweden, 1 sample of *G. granulata* from NW Germany, 1 sample of *G. granulataquadrata* from NW Germany, 13 samples of *G. q. quadrata* from different levels within the Lower Campanian of NW Germany, Belgium, France, and England, 2 samples of *G. quadrata gracilis* from the top Lower Campanian of NW Germany, and 1 sample of *G. quadrata scaniensis* Christensen from the top Lower Campanian of Sweden.

An isometric relationship of the two variates was found in 21 samples. The three samples showing an allometric relationship are *G. quadrata gracilis* from the *conica/gracilis* and *gracilis/mucronata* Zones of Misburg/Höver in NW Germany, respectively, in addition to *G. q. quadrata* from the lower *linqua/quadrata* Zone of the C.P.L. Quarry at Hallembaye in Belgium. In *G. quadrata gracilis* from the *gracilis/mucronata* Zone the growth relationship is strongly allometric, while in *G. quadrata gracilis* from the *conica/gracilis* Zone and *G. q. quadrata* from Hallembaye it is slightly allometric.

2. *Length of guard* vs *dorso-ventral diameter at the alveolar end*. 19 samples were analysed: 3 samples of *G. westfalica*, 1 sample of *G. westfalicagranulata*, 1 sample of *G. granulataquadrata*, 11 samples of *G. q. quadrata*, 2 samples of *G. quadrata gracilis*, and 1 sample of *G. quadrata scaniensis*.

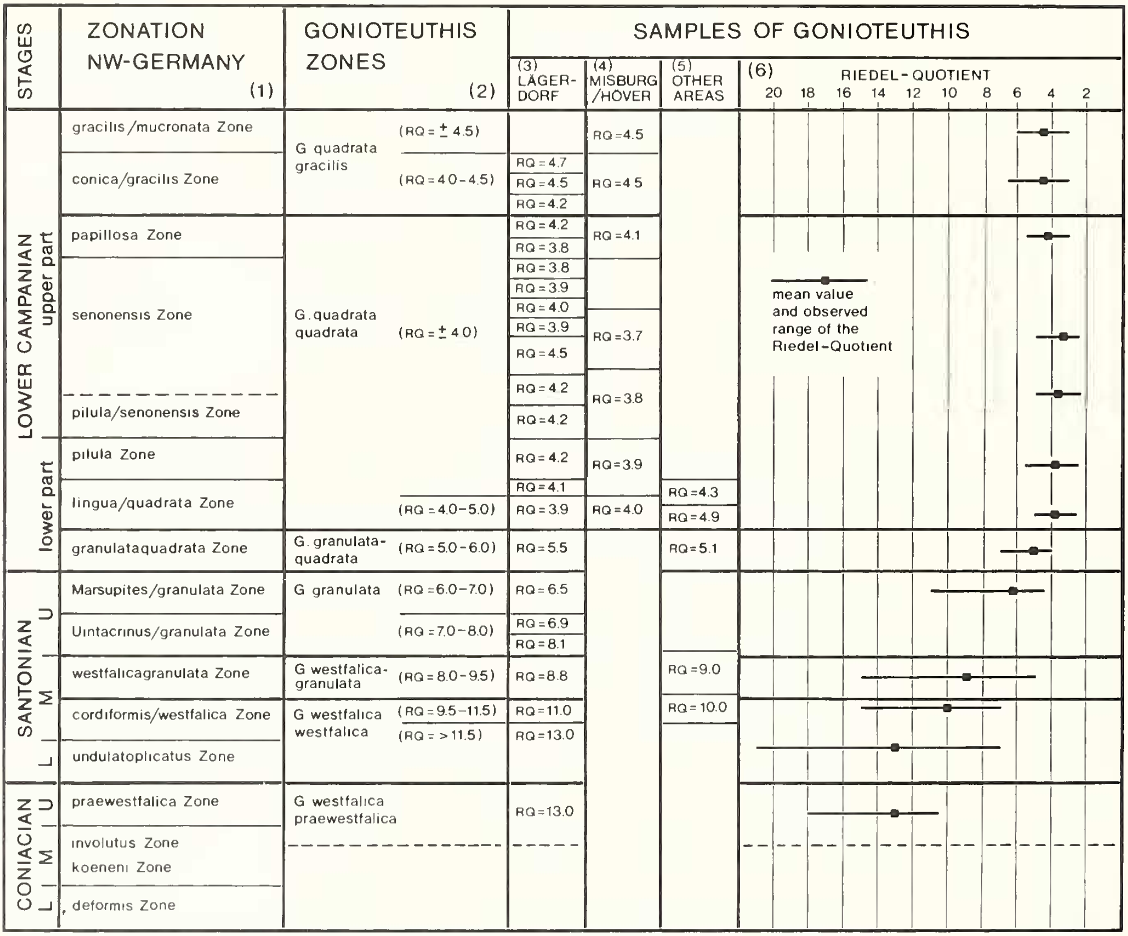
An allometric relationship was found in 12 samples. The seven samples showing an isometric relationship are *G. granulataquadrata* from Weinberg, *G. q. quadrata* from the lower *lingua/quadrata* Zone of Höver and Hallembaye, *G. q. quadrata* from the lower *senonensis* Zone of Höver, in addition to three samples from England and France: Shawford, 'lower course' (middle Lower Campanian); Stiffkey (*papillosa* Zone); and Hardivillers (middle Lower Campanian).

In my opinion, samples of *Gonioteuthis* are better characterized by statistical parameters of the regression analyses than by ratios. Ernst's *Gonioteuthis* zonation based on the mean Riedel Quotient is valid, however, because the relationship of length of guard *vs* depth of pseudoalveolus is isometric in almost all analysed samples of *Gonioteuthis*. The *Gonioteuthis* zonation is discussed further below.

In the analyses of length of guard *vs* dorso-ventral diameter at the alveolar end, the relationship is allometric to strongly allometric in most samples. It is therefore not valid to calculate the mean Slenderness Quotient.

According to Ernst (1964*a*, fig. 12), samples of *G. q. quadrata* and *G. quadrata gracilis* from the upper *senonensis* Zone and above are characterized by having a mean Slenderness Quotient of 6·0 or more, with the mean value increasing stratigraphically upwards. The increasing mean value of the Slenderness Quotient, however, is a function of the allometric relationship of length of guard *vs* dorso-ventral diameter in connection with the diminishing mean length of the guard in samples of *Gonioteuthis* from the upper Lower Campanian. Due to the allometric relationship, small guards are generally more slender than large guards, and consequently the mean Slenderness Quotient will increase when the mean length of the guard decreases.

Phylogeny of Gonioteuthis. The *Gonioteuthis* lineage is an outstanding example of phyletic gradualism, namely slow gradual transformation of a suite of characters within populations through time. The *Gonioteuthis* stock existed for about 10 Ma and the general trend in evolution is the gradual calcification of the anterior part of the guard. In *G. westfalica* the anterior end may be convexly conical, flat, or developed as a shallow pseudoalveolus, while in stratigraphically younger representatives the depth of the pseudoalveolus increases and may be up to one-third of the entire length of the guard. Simultaneously with the development of a deeper pseudoalveolus, the guard becomes increasingly stout and large, reaching a maximum in *G. quadrata*. Another characteristic feature is the gradual development of granulation. The oldest member, *G. westfalica praewestfalica*, does not possess granulation (Ernst and Schulz 1974). The succeeding taxon, *G. w. westfalica*, shows a wide variation with respect to this character; some specimens carry scattered granules on the dorsal and/or ventral side of the guard, while in others the granules appear to be arranged in longitudinal rows. The same pattern is also valid for *G. westfalicagranulata*. In stratigraphically younger species, however, the granulation becomes a very prominent character. In samples of *G. westfalica* the shape of the guard is highly variable, and a great proportion of the guards are lanceolate in ventral view. In younger populations the variation in the shape of the guard is smaller, and guards which are lanceolate in ventral view are relatively rare. The cross-section of the anterior end is oval to pointed oval in *G. westfalica* and subrectangular to subquadrate in stratigraphically younger representatives, with all intermediate stages. In the uppermost Lower Campanian, the genus *Gonioteuthis* is characterized by a return of earlier features; e.g. reduced length of the guard, diminished depth of the pseudoalveolus, and increased slenderness of the guard.



TEXT-FIG. 7. Zonation of the Coniacian–Lower Campanian of NW Germany, *Gonioteuthis* zones, and the mean value and observed range of the Riedel Quotient. Column 2 shows the mean value of the Riedel Quotient of typical samples, column 3 the mean value of small, closely-spaced, samples from the chalk of Lägerdorf, column 4 the mean value of samples from broad stratigraphic horizons of the marls of Misburg/Höver, and column 5 the mean value of samples from Braunschweig and Essen. After Christensen (1988).

Gonioteuthis *zonation*. Ernst (1964*a*) established a *Gonioteuthis* zonation of the upper Coniacian–Lower Campanian, mainly on the basis of the mean Riedel Quotient (Text-fig. 7). The following points should be stressed:

1. In the earliest members variation of the Riedel Quotient is large and this variation gradually diminishes upwards (see column 6).

2. There is a rapid change in the mean Riedel Quotient from the upper Coniacian to the basal Lower Campanian, but virtually no change in stratigraphically younger species. The mean Riedel Quotient is about 4 during most of the Lower Campanian except in the uppermost Lower Campanian. In *G. quadrata gracilis* the mean Riedel Quotient is slightly larger than in *G. q. quadrata* from the middle Lower Campanian. This is due to the allometric relationship of the length of the guard *vs* the depth of the pseudoalveolus in *G. quadrata gracilis* in connection with the diminishing mean length of the guard. Due to allometry, small specimens generally have a shallower pseudoalveolus than large specimens, and consequently the mean Riedel Quotient increases when the mean length decreases. *Gonioteuthis* zonation of the Lower Campanian is therefore hardly workable using only the mean Riedel Quotient. By using other characters, however, it is possible to determine samples of *Gonioteuthis* with some confidence. *G. quadrata gracilis* is smaller than *G. q. quadrata*. Moreover, *G. quadrata gracilis* has notches in the pseudoalveolus and it is more strongly granulated than *G. q. quadrata* from the lower Lower Campanian.

3. Specimens with a very deep pseudoalveolus (Riedel Quotient about 2·5) occur only in the middle Lower Campanian (see column 6).

4. There is a discrepancy between the samples from Lägerdorf and Misburg/Höver in the lower and middle Lower Campanian. The samples from Misburg/Höver generally have a deeper pseudoalveolus (compare columns 3 and 4).

5. A single specimen or some few specimens cannot be assigned safely to a species. For instance, a specimen with a Riedel Quotient of 7 might belong to either *G. w. westfalica*, *G. westfalicagranulata*, *G. granulata*, or *G. granulataquadrata*.

The *Gonioteuthis* zonation of Ernst (1964*a*), was shown to be workable by Ernst (1966, 1968), Ernst and Schulz (1974), Ulbrich (1971), Christensen (1975*a*, *b*, 1986, 1988), and Jarvis (1980).

Distribution. *Gonioteuthis* is known from the Middle Coniacian *I. involutus* Zone to the boundary between the Lower and Upper Campanian, and the extinction level of the genus has been proposed by several authors, including Jeletzky (1958) and Schulz *et al.* (1984), as the boundary between the Lower and Upper Campanian.

The genus had its evolutionary centre in northwestern Europe and is found almost exclusively in the Central European Palaeogeographic Subprovince. A few specimens are reported from the northernmost part of the Tethyan Realm.

Gonioteuthis westfalica praewestfalica Ernst and Schulz, 1974

Plate 1, figs 10–13

1974 *Gonioteuthis westfalica praewestfalica* Ernst and Schulz, p. 49, pl. 5, figs 2–9.
1983*a* *Gonioteuthis praewestfalica* Ernst and Schulz; Bailey *et al.*, p. 35.

Holotype. The specimen figured by Ernst and Schulz (1974, pl. 5, fig. 4) is the holotype.

Material. BGS GSM 118339 from West Cliff, Ramsgate, Kent, *coranguinum* Zone, 10·0–10·5 m beneath Bedwell's Columnar Band (i.e. top Coniacian *sensu* Bailey *et al.* 1984).

Remarks. The subspecies was described in detail by Ernst and Schulz (1974) on the basis of German material. They regarded it as the earliest member of the *Gonioteuthis* lineage, appearing in the Middle and Upper Coniacian chalks of Lägerdorf. They stated that *praewestfalica* can be distinguished from the nominate subspecies only on the basis of biometric analysis of a sample. The main characters separating *praewestfalica* from *westfalica* are the ventrally flattened and club-shaped guard. In addition, *praewestfalica* is not granulated, whereas *westfalica* may be granulated.

The important characters of the English specimen are as follows: length of guard, 49·1 mm; Riedel Quotient, 17·5; Slenderness Quotient, 7·2; maximum lateral diameter divided by the lateral diameter at the alveolar end, 1·2. Moreover, the specimen is not granulated. The specimen falls within the variation of *G. westfalica praewestfalica* and is from the Upper Coniacian. It is therefore referred to as *G. westfalica praewestfalica*.

Distribution. G. westfalica praewestfalica is recorded from NW Germany and England. It occurs in NW Germany in the Middle and Upper Coniacian (Ernst and Schulz 1974). The English specimen came from the Upper Coniacian.

Gonioteuthis westfalica westfalica (Schlüter, 1876)

Plate 1, figs 14–29

Synonymy. See Christensen (1975*a*).

Lectotype. The specimen figured by Schlüter (1876, pl. 53, fig. 10) was designated as lectotype by Ernst and Schulz (1974, p. 50).

Material. BMNH C44381, Micheldever, *coranguinum* Zone; BMNH C7341 and C59277, Grays, *coranguinum* Zone; BMNH C43522–3, Red Lion Pit, Gravesend, *coranguinum* Zone; BMNH C43496–9, C43502, C43504, C43510, C43518 and C43520, Gravesend, *coranguinum* Zone; BMNH C43524, Northfleet, Kent, *coranguinum* Zone; BMNH C43525, North Foreland, Kent, *coranguinum* Zone.

Dimensions.

	L	D	DVDAE	LDAE	MLD	RQ	SQ
BMNH C44381	46·3	3·2	6·8	5·7	7·4	14·5	6·8
BMNH C7341	56·5	1·8	8·2	7·7	9·2	31·4	6·9
BMNH C43522	50·1	3·8	7·8	7·3	9·0	13·2	6·4
BMNH C43496	65·4	4·5	9·9	9·0	10·7	14·5	6·6
BMNH C43497	54·8	6·8	11·0	9·6	11·5	8·1	5·0
BMNH C43498	60*	3·2	9·5	8·5	10·5	18·8	6·3
BMNH C43499	62·2	3·8	9·4	8·6	9·8	16·4	6·6
BMNH C43502	65·4	4·5	10·1	9·3	10·8	14·5	6·5
BMNH C43504	55·3	4·5	9·6	8·2	9·7	12·3	5·8
BMNH C43510	51·2	2·0	—	—	—	25·6	—
BMNH C43518	65·6	4·0	9·0	8·2	10·0	16·4	7·3
BMNH C43520	58*	8·2	11·6	10·3	11·0	7·1	5·0

* = estimated.

Univariate analysis. The mean value, standard deviation, coefficient of variation, and observed range of length of guard (in mm), Riedel Quotient, and Slenderness Quotient of the nine complete specimens from Gravesend are reported below.

Gravesend, Kent:

Character	N	$\bar{X}$	SD	CV	OR
L	9	59·8	5·3	8·9	51·2–65·6
RQ	9	14·8	5·6	37·7	7·1–25·6
SQ	8	6·1	0·8	13·1	5·0–7·3

Remarks. Ernst (1964*a*, 1968) recognized two zones of *G. westfalica* in the Lower and Middle Santonian. The lower zone is characterized by samples of *G. westfalica* having a mean Riedel Quotient above 11·5, and the upper zone by samples with a mean Riedel Quotient between 9·5–11·5 (Text-fig. 7).

The small sample from Gravesend has a mean Riedel Quotient of 14·8, suggesting the lower *G. westfalica* Zone. The large observed range of the Riedel Quotient, however, in connection with the fact that *G. westfalicagranulata* occurs at Gravesend too (see below), may indicate the presence of the upper *G. westfalica* Zone at Gravesend. The specimens from Micheldever, Grays, and the Red Lion Pit are regarded to be from the lower *G. westfalica* Zone on the basis of their Riedel Quotient.

Distribution. G. w. westfalica is very common in NW Germany and Scania. Outside these areas it has been recorded from most parts of the Central European Subprovince except east of Ukraine. It occurs in the Lower and Lower Middle Santonian.

Gonioteuthis westfalicagranulata (Stolley, 1897)

Plate 1, figs 30–37

Synonymy. See Christensen (1975*a*, *b*).

Lectotype. The specimen figured by Stolley (1897, pl. 2, fig. 16; pl. 3, fig. 6) was designated as lectotype and refigured by Christensen (1975*b*, pl. 10, fig. 1; text-fig. 2A).

Material. BGS Zt1960, White Ness, near Kingsgate, Kent, uppermost *coranguinum* Zone immediately below entry of *Uintacrinus*. BMNH C43521, Gravesend, *coranguinum* Zone.

Dimensions.

	L	D	DVDAE	LDAE	MLD	RQ	SQ
BGS Zt1960	50·6	5·6	7·9	7·2	8·1	9·0	6·4
BMNH C43521	60*	9·0	9·9	9·2	9·2	6·7	6·1

* = estimated.

Remarks. BMNH C43521 carries granules and the Riedel Quotient is outside the range of *G. westfalica*. It is therefore tentatively referred to *G. westfalicagranulata*. Zt1960 came from beds correlative with the German *G. westfalicagranulata* Zone and falls within the variation of *G. westfalicagranulata*.

Distribution. The species occurs in the Upper Middle Santonian *G. westfalicagranulata* Zone.

Gonioteuthis granulata (Blainville, 1827)

Synonymy. See Christensen (1975*a*).

Type. Lectotype, here designated, the original of Blainville (1827, pl. 1, fig. 10).

Material. This species occurs fairly commonly at the level of the *Marsupites* acme in east Kent and Sussex (Bailey *et al*. 1983*a*). I have analysed biometrically three small samples: (1) a sample labelled '*Marsupites* band, Northdown brickworks pit, near Margate' (BMNH C42650–5, C42666, C42668–9); (2) a sample labelled '*Marsupites* Zone, Rifle Butts, Margate' (BMNH C43250–1, C43254–7); and (3) a sample labelled '*Marsupites* band, Margate' (BMNH C43242–5, C43248, C43236); all A. W. Rowe Colln.

Univariate analysis.

Northdown brickworks pit:

Character	N	$\bar{X}$	SD	CV	OR
L	9	61·3	6·8	11·1	50·7–71·6
RQ	9	6·5	0·8	11·8	5·5–7·5
SQ	9	5·7	0·5	10·6	4·8–6·4

Rifle Butts:

Character	N	$\bar{X}$	SD	CV	OR
L	6	67·3	7·2	10·7	55·0–81·0
RQ	6	7·4	1·1	15·3	6·6–9·6
SQ	6	6·2	1·1	17·7	4·9–7·9

Margate:

Character	N	$\bar{X}$	SD	CV	OR
L	6	60·8	5·4	8·9	56·3–71·2
RQ	6	7·7	1·3	16·3	6·0–9·1
SQ	6	6·2	0·7	11·0	5·1–6·9

Remarks. Ernst (1964*a*) recognized two zones of *G. granulata* in the Upper Santonian: a lower *Uintacrinus/granulata* Zone characterized by samples of *Gonioteuthis* having a mean Riedel Quotient of 7·0–8·0, and an upper *Marsupites/granulata* Zone defined by samples of *Gonioteuthis* with a mean Riedel Quotient of 6·0–7·0 (Text-fig. 7).

The three samples can be referred to *G. granulata* on the basis of their mean Riedel Quotients. The sample from Northdown brickworks pit has a mean Riedel Quotient of 6·5 and is thus from the upper Santonian *Marsupites/granulata* Zone. The samples from Rifle Butts and Margate have mean Riedel Quotients of 7·4 and 7·7, respectively, suggesting the lower Upper Santonian *Uintacrinus/granulata* Zone. This is at variance with the supposed age given on the labels, a discrepancy possibly due to the small number of specimens in the two samples.

Distribution. *G. granulata* occurs in the Upper Santonian.

Gonioteuthis granulataquadrata (Stolley, 1897)

Synonymy. See Christensen (1975*a*, *b*)

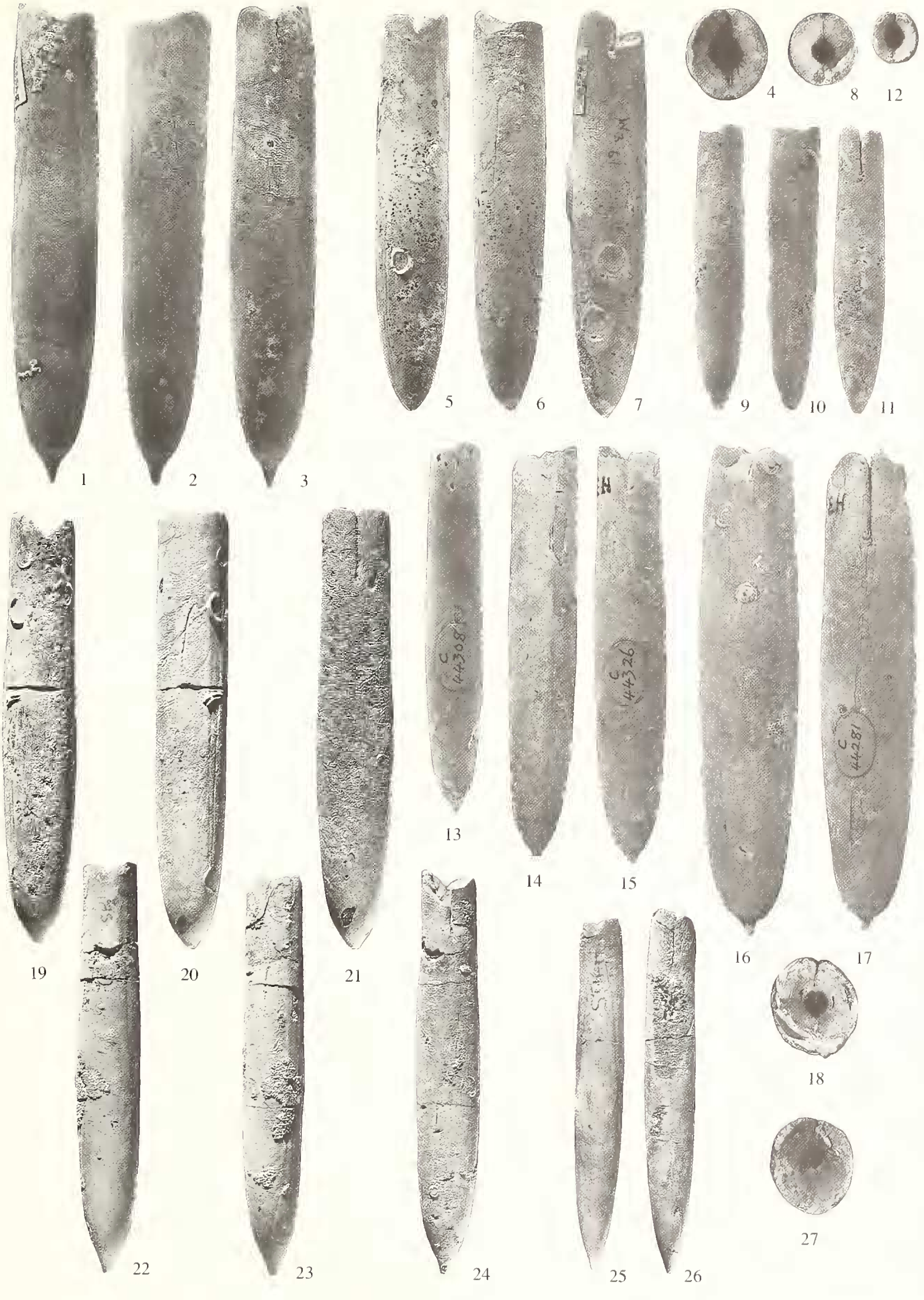
Lectotype. The specimen figured by Stolley (1897, pl. 2, fig. 23; pl. 3, fig. 13) was designated as lectotype and refigured by Christensen (1975*b*, pl. 10, fig. 2; text-fig. 2A).

Material. BMNH C43298, C43000, C43302–4, Banham (pit no. 129 of Rowe), Norfolk.

EXPLANATION OF PLATE 2

Figs 1–27. *Gonioteuthis quadrata quadrata* (Blainville), Wells, Norfolk (1–12); East Harnham, Wiltshire (13–18); and Stiffkey, Norfolk (19–27). 1–4, SM B953241, a large average-shaped specimen, dorsal view; 2, lateral view; 3, ventral view; 4, view of the anterior end. 5–8, SM B95375, a medium-sized specimen with an average shape; 5, dorsal view; 6, lateral view; 7, ventral view; 8, view of the anterior end. 9–12, SM B95323, a small specimen with an average shape; 9, dorsal view; 10, lateral view; 11, ventral view; 12, view of the anterior end. 13, BMNH C44308, a medium-sized guard in ventral view. 14–15, BMNH C44326, a medium-sized guard; 14, lateral view; 15, ventral view. 16–18, BMNH C44281, a large stout specimen; 16, dorsal view; 17, ventral view; 18, view of the anterior end. 19–21, SM B97232, a large specimen; 19, dorsal view; 20, dorsal view; 21, ventral view. 22–24, SM B97237, a slender medium-sized specimen; 22, dorsal view; 23, lateral view; 24, ventral view. 25–27, SM B97247, a small slender specimen; 25, dorsal view; 26, ventral view; 27, view of the anterior end, ×2.

All specimens are coated with ammonium chloride. All figures are natural size unless otherwise stated.



CHRISTENSEN, *Gonioteuthis*

Univariate analysis.

Character	N	$\bar{X}$	SD	CV	OR
L	5	68·0	9·3	13·7	59·4–80·7
RQ	5	5·5	0·8	14·1	4·2–6·1
SQ	5	6·0	0·8	13·4	5·1–6·8

Remarks. According to Ernst (1964*a*) *G. granulataquadrata* has a mean Riedel Quotient of 5·0–6·0 (Text-fig. 7). The small sample from Banham has a mean Riedel Quotient of 5·5 and may be referred to this species.

Distribution. G. granulataquadrata occurs in the basal Lower Campanian (*G, granulataquadrata* Zone).

Gonioteuthis quadrata quadrata (Blainville, 1827)

Plate 2, figs 1–27

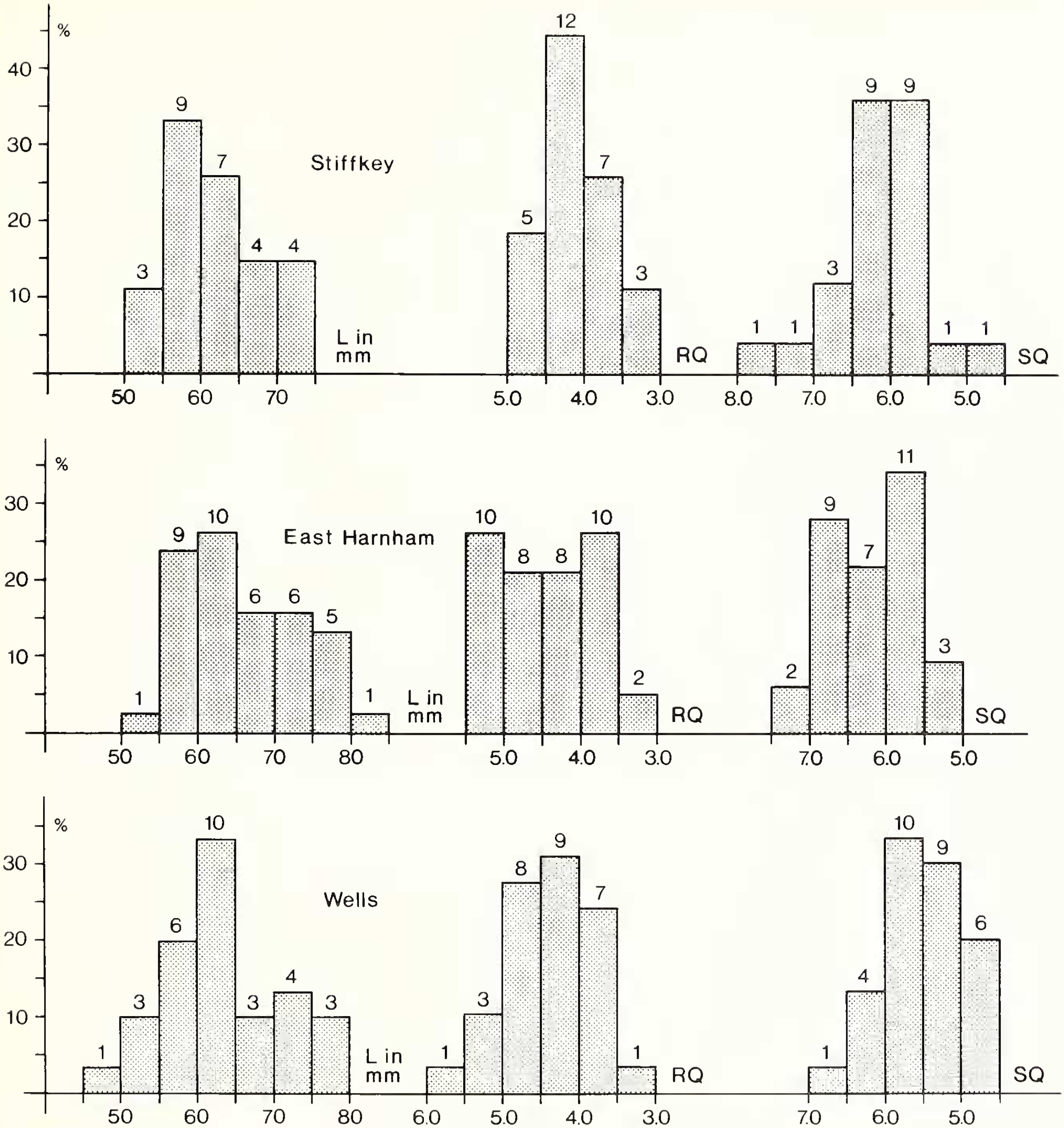
1827 *Belemnites quadratus* Blainville, p. 62, pl. 1, fig. 9.
1878 *Gonioteuthis quadrata* (Blainville); Bayle, pl. 23, figs 6–8.
1892 *Actinocamax quadratus* (Blainville) var. *ampullacea* Stolley, p. 232, pl. 8, fig. 1.
1892 *Actinocamax quadratus* (Blainville) var. *oblonga* Stolley, p. 233, pl. 7, fig. 5.
1897 *Actinocamax quadratus* (Blainville); Stolley, p. 284, pl. 2, fig. 24; pl. 3, fig. 14.
1952 *Gonioteuthis quadrata* (Blainville) var. *cylindrica* Naidin, p. 81, pl. 5, figs 4 and 6; pl. 7, fig. 5.
1964*a* *Gonioteuthis quadrata quadrata* (Blainville); Ernst, pl. 1, figs 6 and 7; pl. 2, figs 5 and 6; pl. 4, fig. 1.
1971 *Gonioteuthis quadrata quadrata* (Blainville); Ulbrich, pl. 1, Reihe 1, figs 1–16, Reihe 2, figs 1–14, Reihe 3, figs 1–8.
1980 *Gonioteuthis quadrata quadrata* (Blainville); Jarvis, pl. 116, figs 1–15.
1987 *Gonioteuthis quadrata quadrata* (Blainville); Christensen and Schmid, p. 16, pl. 3, figs 8–11.

Type. Lectotype, here designated, the original of Blainville (1827, pl. 1, fig. 9).

Material. Wells: 30 near-complete specimens, *E. depressula* Subzone of the *O. pilula* Zone, Hammond Colln, SM B95314–15, B95318–24, B95328, B95330–35, B95338–39, B95341–42, B95345–47, B95351, B95353, B95367–70, B95375, B95382; Stiffkey: 27 near-complete specimens, higher part of the *Gonioteuthis* Zone, Hammond Colln, SM B97232–48, B97250, B97252–56, B97263, B97268–69, B97273; East Harnham: 38 near-complete specimens, top *pilula* Zone or base of *quadrata* Zone, Blackmore Colln, BMNH C44260, C44266, C44272–73, C44275–76, C44281–87, C44290, C44293, C44299–305, C44307–09, C44314, C44322, C44326, C44330, C44332, C44336–37, C59164, C59167–68, C59170–71; Shawford, 'lower course', *quadrata* Zone: 15 near-complete specimens, Brydone Colln, BGS GSM 101087, 101090–91, 101093, 101096, 101098–103, 101106, 101108–11. In addition, I have seen many apical fragments from these localities.

Univariate analyses. The mean value, standard deviation, coefficient of variation, and observed range of the length of the guard, the Riedel Quotient, and the Slenderness Quotient are shown in Table 2. Histograms for the samples from Stiffkey, Wells, and East Harnham are shown in Text-figure 8. Histograms were not made for Shawford owing to the small number of specimens. The size-frequency distributions were tested for normality using the Kolmogorov–Smirnov test for goodness of fit, and none of the distributions differed significantly from normal (see Table 3). It should be emphasized that juvenile specimens are absent in the samples. On the basis of the univariate analyses the samples can be regarded as homogeneous.

Bivariate analyses. Scatter plots of the length of the guard *vs* the depth of the pseudoalveolus, and the length of the guard *vs* the dorso-ventral diameter at the alveolar end of the samples are shown in Text-figures 9–12, as are the regression lines. The equation of the regression lines are shown in Table 4. Values of the correlation coefficients are very highly significant ($P < 0{\cdot}001$ with N–2 degrees of freedom). The y-intercepts were tested by the t-test to see if they differed significantly from zero. In two cases, Wells and East Harnham, the t_a-values are significant ($0{\cdot}02 > P > 0{\cdot}01$, with N–2 degrees of freedom), implying an allometric relationship of the



TEXT-FIG. 8. Histograms of the length of the guard (L), Riedel Quotient (RQ), and Slenderness Quotient (SQ) of three samples of *Gonioteuthis quadrata quadrata* from Stiffkey, East Harnham, and Wells. The figures above the bars are the actual number of specimens.

length of the guard with the dorso-ventral diameter at the alveolar end. In the other cases, the *y*-intercepts do not differ significantly from zero at the 5% level, implying an isometric relationship of the variates.

On the basis of these bivariate analyses, the samples are regarded as homogeneous, which is consistent with the univariate analyses.

Remarks. The mean values of the length of guard are of little taxonomic value, because juvenile specimens are absent in all samples. On the basis of the histograms and observed ranges of the

WELLS

Character	N	$\overline{X}$	SD	CV	OR
L	30	63.8	8.2	12.8	45.1-80.0
RQ	29	4.4	0.6	14.0	3.4- 5.9
SQ	30	5.6	0.5	9.2	4.7- 6.8

EAST HARNHAM

Character	N	$\overline{X}$	SD	CV	OR
L	38	66.3	7.3	11.0	54.0-83.3
RQ	38	4.5	0.6	13.9	3.4- 5.5
SQ	32	6.2	0.6	9.0	5.0- 7.5

SHAWFORD, 'lower course'

Character	N	$\overline{X}$	SD	CV	OR
L	15	66.9	7.2	10.8	53.0-78.8
RQ	15	4.4	0.5	12.4	3.5- 5.4
SQ	13	6.0	0.5	7.7	5.3- 7.1

STIFFKEY

Character	N	$\overline{X}$	SD	CV	OR
L	27	62.7	6.5	10.3	51.8-75.0
RQ	27	4.1	0.4	10.1	3.2- 4.8
SQ	25	6.2	0.6	9.4	4.9- 7.6

TABLE 2. Univariate analyses of four samples of *Gonioteuthis quadrata quadrata* from Wells, East Harnham, Shawford, 'lower course', and Stiffkey. L = length of the guard; RQ = Riedel Quotient; SQ = Slenderness Quotient; N = number of specimens, $\overline{X}$ = mean value; SD = standard deviation; CV = coefficient of variation; and OR = observed range.

length of the guard, it is obvious, nevertheless, that the specimens from Stiffkey generally are smaller than the specimens from the other samples.

The regression lines of the length of the guard *vs* the depth of the pseudoalveolus of the four samples are shown in Text-figure 13. The samples from Shawford and Wells were compared and *t*-tests showed that the two samples do not differ significantly at the 5% level. As regards Wells *vs* Stiffkey and East Harnham *vs* Stiffkey, *t*-tests showed that the positions of the regression lines are significantly different ($0{\cdot}05 > P > 0{\cdot}01$, with N–2 degrees of freedom). The specimens from Stiffkey and Shawford generally have a deeper pseudoalveolus than the specimens from Wells and East Harnham. The regression lines of the length of the guard *vs* the dorso-ventral diameter at the alveolar end of the four samples are shown in Text-figure 14 from which it is obvious that the samples from East Harnham, Shawford, and Stiffkey are virtually identical. On the other hand, the specimens from Wells are stouter. The samples from Wells and Stiffkey were compared and the *t*-

WELLS

Character	N	D	Probability
L	30	0.1200	P > 0.50
RQ	29	0.0583	P > 0.50
SQ	30	0.1067	P > 0.50

EAST HARNHAM

Character	N	D	Probability
L	38	0.1105	P > 0.50
RQ	38	0.1111	P > 0.50
SQ	32	0.1125	P > 0.50

STIFFKEY

Character	N	D	Probability
L	27	0.1104	P > 0.50
RQ	27	0.0815	P > 0.50
SQ	25	0.0984	P > 0.50

TABLE 3. Results of the Kolmogorov–Smirnov tests for goodness of fit for three samples of *Gonioteuthis quadrata quadrata* from Wells, East Harnham, and Stiffkey.

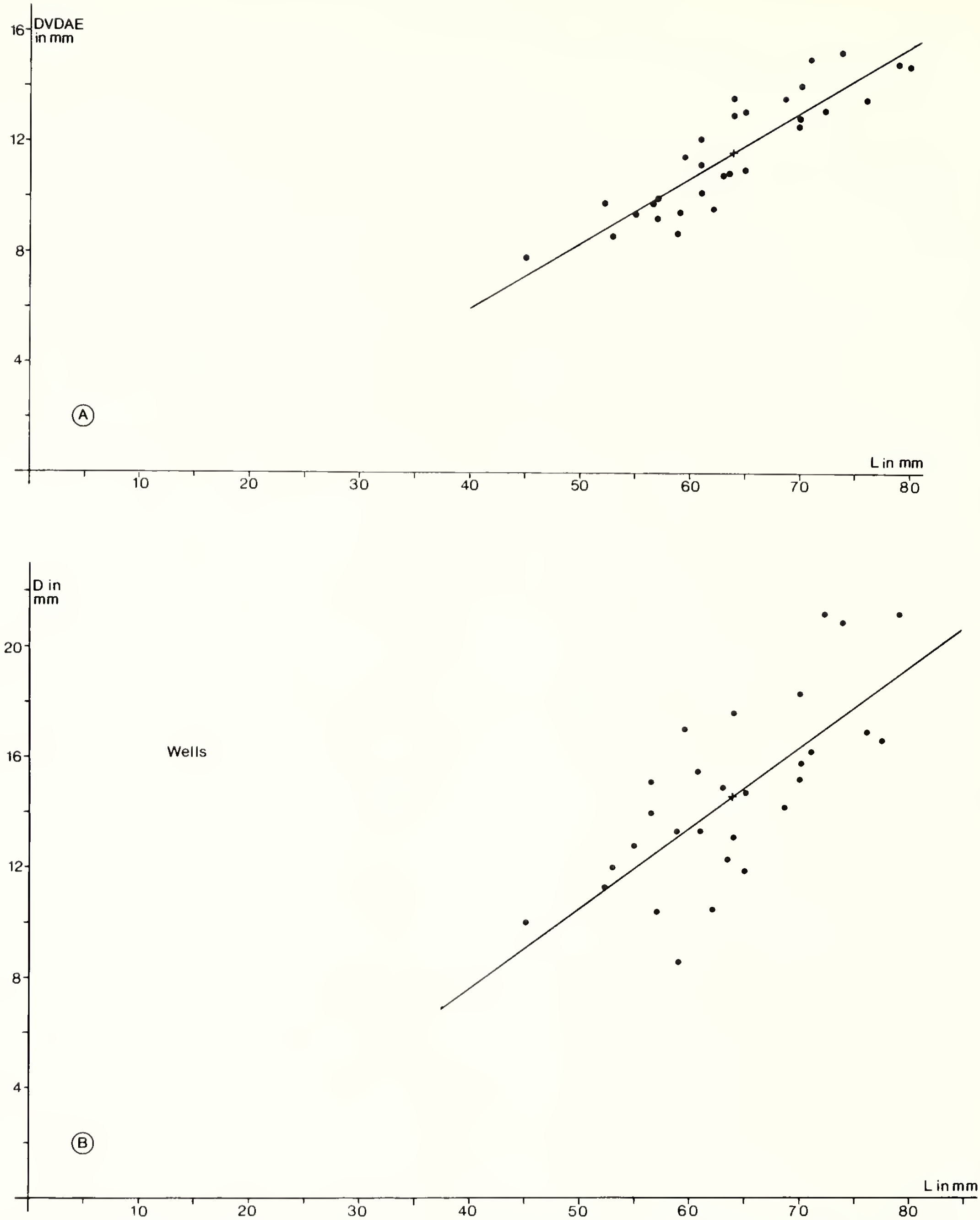
test showed that the difference of the positions is very highly significant ($P < 0{\cdot}001$ with 51 degrees of freedom).

In conclusion, the specimens from Stiffkey are generally smaller, more slender, and have a deeper pseudoalveolus than the specimens from Wells. The specimens from East Harnham and Shawford are virtually identical with respect to the analysed characters. As regards the shape of the guard, the samples from East Harnham and Shawford cannot be differentiated from the sample from Stiffkey. With respect to the depth of the pseudoalveolus in relation to the length of the guard there is a slight difference between East Harnham and Stiffkey; the specimens from Stiffkey have a deeper pseudoalveolus.

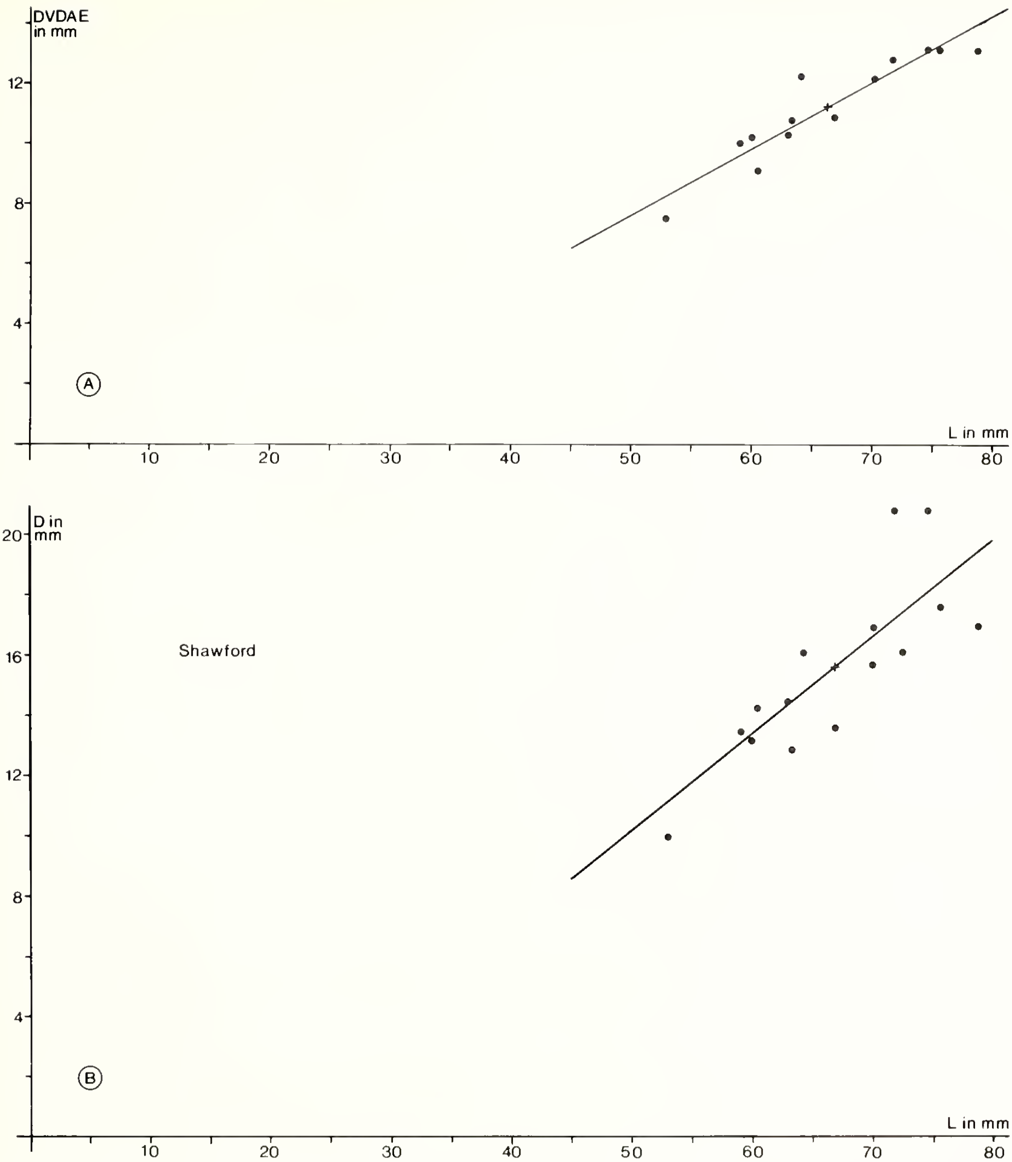
Comparisons. The four samples from England were compared to seven German samples described by Ernst (1964*a*, *b*) and two samples from Belgium and France. The sample from the C.P.L. Quarry at Hallembaye, Belgium was described by Christensen and Schmid (1987), and the sample from Hardivillers, France was described by Jarvis (1980), and was remeasured for the present study. The results of the univariate analyses of the nine samples are shown in Table 5, and the equations of the regression lines are reported in Table 6.

1. *Wells*. The sample from Wells was compared to samples of *G. q. quadrata* from Bremer and Hallembaye from the lower part of the *lingua/quadrata* Zone.

The maximum length of the guard is about 80 mm in the three samples, as in samples of *Gonioteuthis* from the lower and upper parts of the Lower Campanian of NW Germany (Ernst 1964*a*, fig. 8). As regards the length of the guard *vs* the depth of the pseudoalveolus, the sample from Wells does not differ significantly at the 5% level from the Bremer and Hallembaye samples. With regard to the length of the guard *vs* the dorso-ventral diameter at the alveolar end, the positions of the regression lines of the Wells and Hallembaye samples differ significantly ($0{\cdot}05 > P > 0{\cdot}025$, with 84 degrees of freedom). The specimens from Wells are generally stouter than the specimens from Hallembaye.



TEXT-FIG. 9. Scatter plots and regression lines for *Gonioteuthis quadrata quadrata* from Wells. A, length of the guard (L) *vs* dorso-ventral diameter at the alveolar end (DVDAE). B, length of the guard (L) *vs* depth of the pseudoalveolus (D). + = mean value.



TEXT-FIG. 10. Scatter plots and regression lines for *Gonioteuthis quadrata quadrata* from Shawford. A, length of guard *vs* dorso-ventral diameter at the alveolar end (DVDAE). B, length of the guard (L) *vs* depth of the pseudoalveolus (D). + = mean value.

On the basis of the comparisons made above, the sample from Wells is referred to *G. q. quadrata* and is considered to be from the lower part of the *lingua/quadrata* Zone, as are the samples from Bremer and Hallembaye.

2. *Stiffkey*. The sample from Stiffkey was compared to samples of *G. q. quadrata* and *G. quadrata gracilis* from the upper *senonensis*, *papillosa*, and *conica/gracilis* Zones of Höver/Misburg.

The maximum length of guard in the Stiffkey sample is 75 mm, as in German samples of *Gonioteuthis* from the upper part of the Lower Campanian (Ernst 1964*a*, fig. 8). As regards the length of the guard *vs* the depth

WELLS

$y = a + bx$	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -3.9641 + 0.2903L	29	0.7387	P < 0.001	3.1438	0.0488	2.1277	0.9659	0.40 > P > 0.30
DVDAE = -3.6437 + 0.2394L	30	0.9025	P < 0.001	1.4270	0.0222	0.9745	2.5534	0.02 > P > 0.01

EAST HARNHAM

$y = a + bx$	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -2.7180 + 0.2697L	38	0.6762	P < 0.001	3.2645	0.0491	2.1736	0.8326	0.50 > P > 0.40
DVDAE = -3.7598 + 0.2203L	32	0.8609	P < 0.001	1.4334	0.0219	0.8244	2.6230	0.02 > P > 0.01

SHAWFORD, 'lower course'

$y = a + bx$	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -5.8376 + 0.3193L	15	0.7693	P < 0.001	4.9853	0.0741	2.0056	1.1710	0.30 > P > 0.25
DVDAE = -3.3254 + 0.2191L	13	0.9356	P < 0.001	1.6986	0.0255	0.6676	1.9577	0.10 > P > 0.05

STIFFKEY

$y = a + bx$	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -4.0218 + 0.3088L	27	0.7671	P < 0.001	3.2297	0.0513	1.6867	1.2453	0.25 > P > 0.20
DVDAE = -2.4907 + 0.2042L	25	0.8110	P < 0.001	1.9224	0.0307	0.9492	1.2956	0.25 > P > 0.20

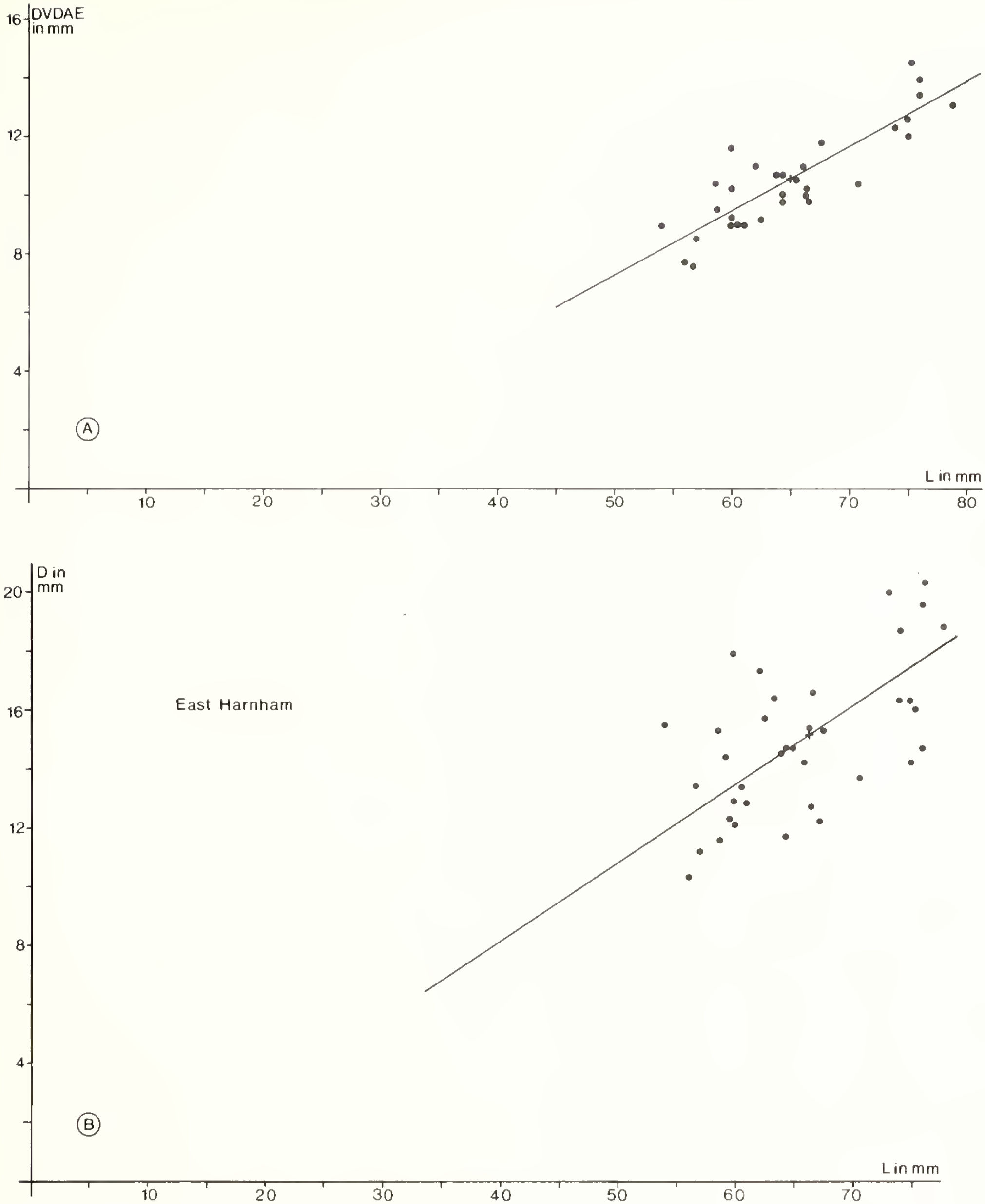
TABLE 4. Estimates of the statistical parameters of four regression analyses of samples of *Gonioteuthis quadrata quadrata* from Wells, East Harnham, Shawford, 'lower course', and Stiffkey. L = length of the guard; D = depth of the pseudoalveolus; DVDAE = dorso-ventral diameter at the anterior end.

of the pseudoalveolus, the Stiffkey sample cannot be differentiated statistically at the 5% level from the samples from the *papillosa* and *conica/gracilis* Zones. The position of the regression lines of the samples from Stiffkey and the upper *senonensis* Zone differ significantly ($P < 0{\cdot}001$, with 77 degrees of freedom). The specimens from the upper *senonensis* Zone have a deeper pseudoalveolus than the specimens from Stiffkey. With respect to the length of the guard *vs* the dorso-ventral diameter at the alveolar end, the Stiffkey sample cannot be differentiated statistically at the 5% level from the samples from the upper *senonensis*, *papillosa*, or *conica/gracilis* Zones.

In conclusion, the sample from Stiffkey cannot be differentiated statistically from *G. q. quadrata* from the *papillosa* Zone or *G. quadrata gracilis* from the *conica/gracilis* Zone. However, the Stiffkey belemnites do not possess notches in the pseudoalveolus, as in *G. quadrata gracilis*, and are therefore referred to *G. q. quadrata* and regarded to be from the *papillosa* Zone.

3. *East Harnham and Shawford*. The two samples are virtually identical with respect to the shape of the guard and the depth of the pseudoalveolus (see above), and therefore only the sample from East Harnham was compared with other samples of *Gonioteuthis*.

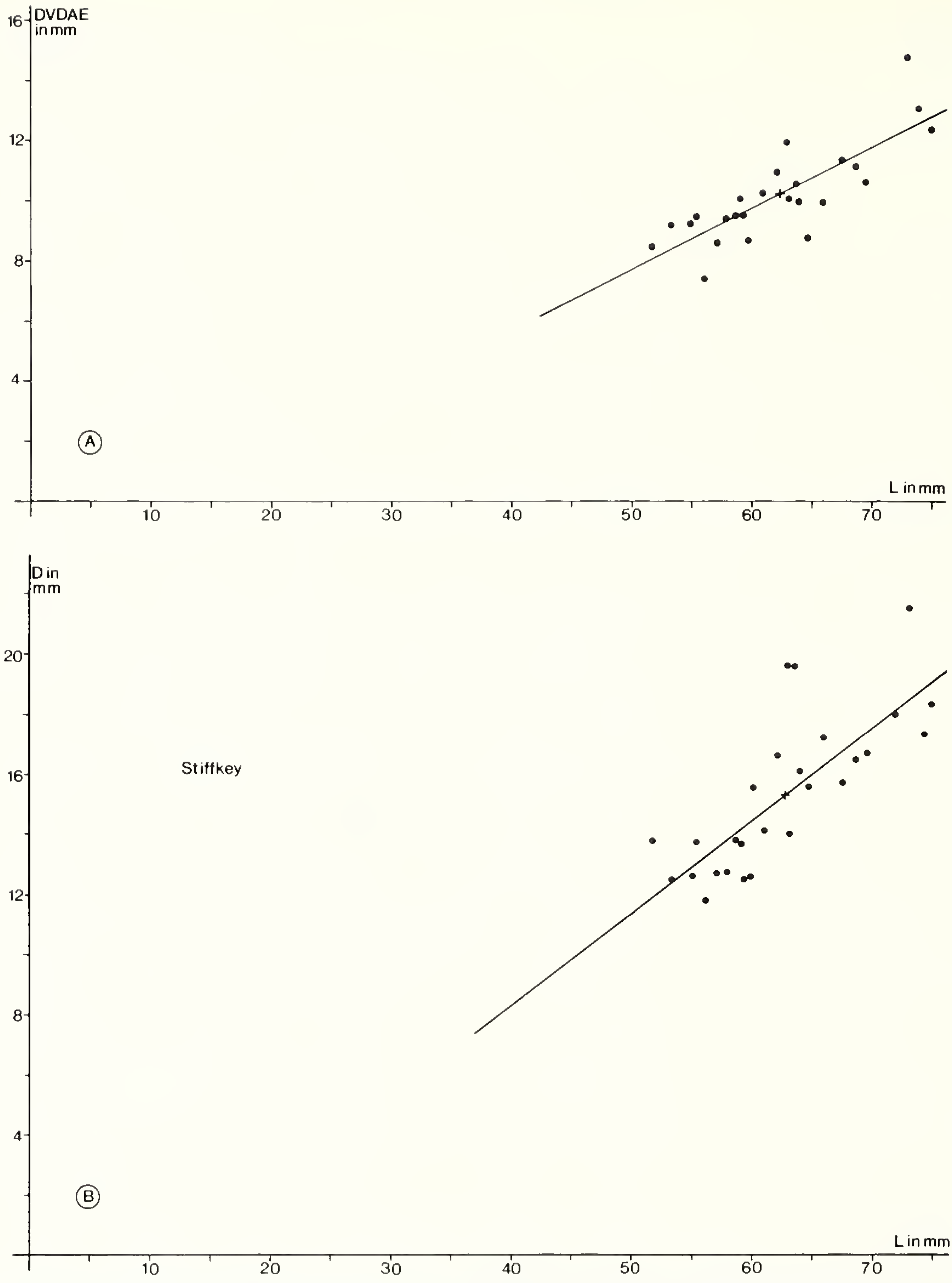
On the basis of the maximum length of the guard it is suggested that the two samples are from the middle Lower Campanian (cf. Ernst 1964*a*, fig. 8). As regards the length of the guard *vs* the depth of the pseudoalveolus, the sample from East Harnham was compared to samples of *G. q. quadrata* from Hallembaye and Bremer (lower part of the *lingua/quadrata* Zone), Höver (upper *lingua/quadrata* Zone to *pilula* Zone), and Hardivillers (*pilula* Zone *sensu anglico*), in addition to *G. quadrata gracilis* from the *conica/gracilis* Zone of Höver. The East Harnham sample does not differ significantly at the 5% level from the samples of *G. q. quadrata* from Hallembaye, Bremer, and Hardivillers, or *G. quadrata gracilis* from the *conica/gracilis* Zone of Höver. In the case of the comparison of East Harnham and Hallembaye, the variances were found to differ significantly ($F = 2{\cdot}0100$ with 36 and 56 degrees of freedom; $0{\cdot}01 > P > 0{\cdot}005$); the test for non-equal



TEXT-FIG. 11. Scatter plots and regression lines for *Gonioteuthis quadrata quadrata* from East Harnham. A, length of the guard (L) *vs* dorso-ventral diameter at the alveolar end (DVDAE). B, length of the guard (L) *vs* depth of the pseudoalveolus (D). + = mean value.

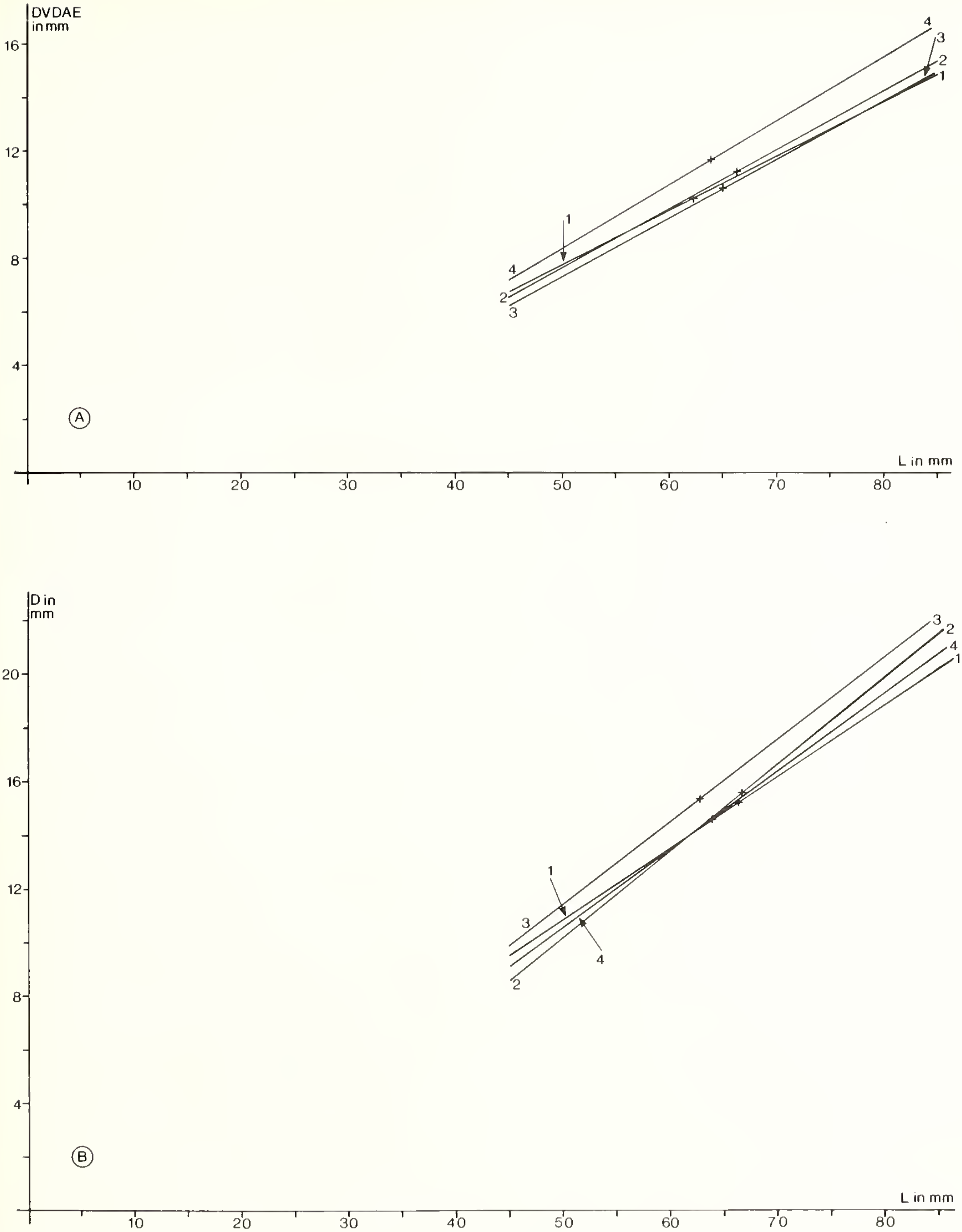
variances was therefore used. The difference of the positions of the regression lines of the samples from East Harnham and *G. q. quadrata* from the upper *lingua/quadrata* Zone to *pilula* Zone is very highly significant ($P < 0{\cdot}001$ with 101 degrees of freedom); specimens from the upper *lingua/quadrata* Zone to *pilula* Zone generally have a deeper pseudoalveolus than the specimens from East Harnham.

With respect to the length of the guard *vs* the dorso-ventral diameter at the alveolar end, the East Harnham



TEXT-FIG. 12. Scatter plots and regression lines for *Gonioteuthis quadrata quadrata* from Stiffkey. A, length of the guard *vs* (L) dorso-ventral diameter at the alveolar end (DVDAE). B, length of the guard (L) *vs* depth of the pseudoalveolus (D). + = mean value.

sample was compared to samples of *G. q. quadrata* from Hallembaye, Hardivillers, and the lower *senonensis* Zone of Höver, in addition to *G. quadrata gracilis* from the *conica/gracilis* Zone of Höver. The East Harnham sample does not differ significantly at the 5% level from the samples from Hardivillers and the *conica/gracilis* Zone. On the other hand, East Harnham *vs* Hallembaye and East Harnham *vs* the lower *senonensis* Zone of



TEXT-FIG. 13. Regression lines of four samples of *Gonioteuthis quadrata quadrata*. A, length of the guard (L) *vs* dorso-ventral diameter at the alveolar end (DVDAE). B, length of the guard (L) *vs* depth of the pseudoalveolus (D). + = mean values. 1, East Harnham; 2, Shawford; 3, Stiffkey; 4, Wells.

Höver comparisons showed that the differences in positions of the regression lines are very highly significant ($P < 0{\cdot}001$). The specimens from Hallembaye and the lower *senonensis* Zone are generally stouter than the East Harnham specimens.

In conclusion, the sample from East Harnham cannot be differentiated with respect to slenderness of the guard and depth of the pseudoalveolus from samples of *G. q. quadrata* from Hardivillers, and *G. quadrata gracilis* from the *conica/gracilis* Zone of Höver. The East Harnham specimens are generally more slender than the specimens from Hallembaye and have a shallower pseudoalveolus than the specimens from the upper *lingua/quadrata* Zone to *pilula* Zone of Höver.

The samples from East Harnham, Shawford, and Hardivillers, however, are not to be referred to *G. quadrata gracilis*, because the maximum length of the guard is larger than in *G. quadrata gracilis*, and they do not possess notches in the pseudoalveolus as in *G. quadrata gracilis*. Moreover, the English top *pilula* Zone and basal *quadrata* Zone are not to be correlated with the German *conica/gracilis* Zone (see Text-fig. 1).

On the basis of the maximum length of the guard and the slenderness of the guard, in addition to the mean Riedel Quotient (4·5 in the East Harnham sample, 4·4 in the Shawford sample, and 4·3 in the Hardivillers sample) (see Table 5), the three samples are regarded as middle Lower Campanian. In samples of *G. q. quadrata* from the middle Lower Campanian of Lägerdorf the mean value of the Riedel Quotient varies from 4·2–4·5 (see Text-fig. 7); these samples have thus a more shallow pseudoalveolus than contemporaneous samples from Misburg/Höver.

Gonioteuthis quadrata gracilis? (Stolley, 1892)

1892 *Actinocamax quadratus* var. *gracilis* Stolley, p. 234, pl. 7, fig. 6.
1952 *Gonioteuthis quadrata* var. *gracilis* (Stolley); Naidin, p. 79, pl. 4, fig. 3; pl. 5, fig. 5; pl. 6, fig. 5.
1964*a* *Gonioteuthis quadrata gracilis* (Stolley); Ernst, p. 166, pl. 1, fig. 8; pl. 2, figs 7–10.

Type. Lectotype, here designated, the original of Stolley (1892, pl. 7, fig. 6).

Material. BMNH C43330 from Attlebridge, and BMNH C43351 from Ringland, Norfolk.

Dimensions.

	L	D	DVDAE	LDAE	MLD	RQ	SQ
BMNH C43330	56·6	9·9	8·7	8·0	8·0	5·7	6·5
BMNH C43351	73·9	19·9	13·1	11·8	12·4	3·7	5·6

Remarks. *G. quadrata gracilis* is distinguished from the nominate subspecies by being smaller and slenderer, with a shallower pseudoalveolus. Moreover, the edge of the pseudoalveolus often has dorsal, lateral, and ventral notches.

The two specimens from Norfolk are tentatively referred to *G. quadrata gracilis* on the basis of their slender guards. Moreover, Peake and Hancock (1961) placed Attlebridge at the top of the *Gonioteuthis* Zone, and Wood (1988) placed Ringland very high in the same zone.

Distribution. *G. quadrata gracilis* occurs in the upper Lower Campanian *conica/gracilis* and *gracilis/mucronata* Zones.

Genus BELEMNELLOCAMAX Naidin, 1964
[= *Actinocamax* (*Paractinocamax*) Naidin, 1964, p. 62]

Type species. *Belemnites mammillatus* Nilsson, 1826 by original designation.

Diagnosis. See Christensen (1975*a*).

Remarks. The evolutionary lineage of *Belemnellocamax*, in ascending order, *B.* ex gr. *grossouvrei* (Janet, 1891), *B. mammillatus* (Nilsson, 1826), and *B. balsvikensis* (Brotzen, 1960), was studied by Christensen (1975*a*, 1976, 1986). The general trend in evolution is the gradual calcification of the anterior end of the guard. Moreover, the guard becomes more slender and less lanceolate through time. Normally, the genus is not granulated, but a few granulated specimens of *B.* ex gr. *grossouvrei* and *B. mammillatus* have been recorded (cf. Christensen 1986).

BREMER, lower part of lingua/quadrata Zone

Character	N	$\bar{X}$	SD	CV	OR
L	38	67.3	6.4	9.5	58.5-82.5
RQ	38	4.6	0.6	13.1	3.7- 6.3

HALLEMBAYE, lower part of lingua/quadrata Zone

Character	N	$\bar{X}$	SD	CV	OR
L	60	67.3	7.2	10.7	52.0-80.3
RQ	58	4.5	0.5	11.1	3.5- 5.9

HÖVER, upper part of lingua/quadrata Zone

Character	N	$\bar{X}$	SD	CV	OR
L	24	60.3	10.5	17.4	41.0-78.5
RQ	24	4.0	0.5	12.2	2.8- 4.9

HÖVER, upper lingua/quadrata Zone to pilula Zone

Character	N	$\bar{X}$	SD	CV	OR
L	67	60.9	9.8	16.1	40.0-81.5
RQ	67	4.1	0.5	11.2	2.8- 5.4

HÖVER, lower senonensis Zone

Character	N	$\bar{X}$	SD	CV	OR
L	47	64.1	9.2	14.3	47.3-85.0
RQ	47	3.8	0.5	12.6	2.9- 4.9

HÖVER, upper senonensis Zone

Character	N	$\bar{X}$	SD	CV	OR
L	54	64.3	9.5	14.7	39.0-80.5
RQ	54	3.7	0.4	12.0	2.6- 4.6

HÖVER, papillosa Zone

Character	N	$\bar{X}$	SD	CV	OR
L	28	61.8	9.1	14.7	44.7-78.0
RQ	27	4.0	0.5	12.5	3.3- 5.0

HÖVER, conica/gracilis Zone

Character	N	$\bar{X}$	SD	CV	OR
L	65	57.8	6.9	12.0	41.0-73.0
RQ	65	4.5	0.6	14.1	3.4- 6.4

HARDIVILLERS, middle Lower Campanian

Character	N	$\bar{X}$	SD	CV	OR
L	61	65.8	6.7	10.2	50.0-86.6
RQ	61	4.3	0.5	12.6	3.2- 5.5

TABLE 5. Univariate analyses of nine samples of *Gonioteuthis quadrata quadrata* and *G. quadrata gracilis*. L = length of the guard; RQ = Riedel Quotient; N = number of specimens; $\bar{X}$ = mean value; SD = standard deviation; CV = coefficient of variation; and OR = observed range.

BREMER, lower part of lingua/quadrata Zone

y = a + bx	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -3.1563 + 0.2687L	38	0.6924	P < 0.001	3.1534	0.0467	1.8027	1.0009	0.30 > P > 0.25

HALLEMBAYE, lower part of lingua/quadrata Zone

y = a + bx	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -4.6948 + 0.2970L	58	0.8192	P < 0.001	1.8903	0.0280	1.5332	2.4836	0.02 > P > 0.01
DVDAE = -2.4293 + 0.2136L	58	0.8326	P < 0.001	1.2636	0.0187	1.0293	1.9225	0.10 > P > 0.05

HÖVER, upper part of lingua/quadrata Zone

y = a + bx	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -0.8883 + 0.2685L	24	0.7982	P < 0.001	2.6404	0.0432	2.1657	0.3364	0.80 > P > 0.70
DVDAE = -1.8504 + 0.2018L	24	0.9193	P < 0.001	1.1258	0.0184	0.9234	1.6437	0.20 > P > 0.10

HÖVER, upper lingua/quadrata Zone to pilula Zone

y = a + bx	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -1.7270 + 0.2770L	67	0.8393	P < 0.001	1.3722	0.0223	1.7695	1.2586	0.25 > P > 0.20
DVDAE = -2.6490 + 0.2136L	67	0.9517	P < 0.001	0.5273	0.0086	0.6800	5.0236	P < 0.001

HÖVER, lower senonensis Zone

y = a + bx	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -4.1994 + 0.3336L	47	0.8033	P < 0.001	2.4022	0.0371	2.3022	1.7482	0.10 > P > 0.05
DVDAE = -1.7965 + 0.2011L	46	0.9031	P < 0.001	0.9273	0.0143	0.8886	1.9374	0.10 > P > 0.05

HÖVER, upper senonensis Zone

y = a + bx	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -3.3223 + 0.3286L	54	0.8248	P < 0.001	2.0134	0.0310	2.1343	1.6501	0.20 > P > 0.10
DVDAE = -3.4106 + 0.2224L	53	0.8960	P < 0.001	0.9749	0.0149	1.0066	3.4984	P < 0.001

HÖVER, papillosa Zone

y = a + bx	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -4.9266 + 0.3353L	27	0.8582	P < 0.001	2.5120	0.0403	1.9013	1.9612	0.10 > P > 0.05
DVDAE = -3.1714 + 0.2127L	26	0.9014	P < 0.001	1.2719	0.0205	0.8210	2.4933	0.02 > P > 0.01

HÖVER, conica/gracilis Zone

y = a + bx	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -3.7756 + 0.2917L	65	0.7649	P < 0.001	1.8000	0.0309	1.7110	2.0977	0.05 > P > 0.025
DVDAE = -2.5297 + 0.2028L	65	0.9013	P < 0.001	0.7138	0.0123	0.6785	3.5442	P < 0.001

HARDIVILLERS, middle Lower Campanian

y = a + bx	N	r	Probability	SD_a	SD_b	SD_{yx}	t_a	Probability
D = -3.7036 + 0.2944L	61	0.7271	P < 0.001	2.2900	0.0340	1.7676	1.6173	0.20 > P > 0.10
DVDAE = -0.6492 + 0.1778L	59	0.8146	P < 0.001	1.0922	0.0165	0.8569	0.5944	0.60 > P > 0.50

TABLE 6. Estimates of the statistical parameters of nine regression analyses of samples of *Gonioteuthis quadrata quadrata* and *G. quadrata gracilis*. L = length of the guard; D = depth of the pseudoalveolus; DVDAE = dorso-ventral diameter of the anterior end.

Naidin (1964) placed the *grossouvrei* group in *Actinocamax* (*Paractinocamax*), type species *Actinocamax grossouvrei* Janet, while *mammillatus* was placed in *Belemnellocamax*. The classification of Naidin was fully discussed by Christensen (1986) and is not followed here. The subgenus *Paractinocamax* was considered a junior synonym of *Belemnellocamax*.

Distribution. *B.* ex gr. *grossouvrei* is widely distributed but rare in the North European Province. *B. mammillatus* is extremely common in Scania, but rare outside this area; it has been recorded from northern Germany, Poland, and the eastern part of the Russian Platform. *B. balsvikensis* also occurs commonly in Scania, but outside this area it is unknown except for a find of two specimens from NW Germany (Christensen and Schulz 1976). It can thus be concluded that the area of distribution of the genus *Belemnellocamax* gradually diminished through its stratigraphic range.

Belemnellocamax is recorded from the lower Santonian (possibly highest Coniacian) to the lower Upper Campanian (Christensen 1986).

Belemnellocamax ex gr. *grossouvrei* (Janet, 1891)

Plate 3, figs 1–21

Material. BMNH C42818, West Harnham, top *pilula* Zone-basal *quadrata* Zone, (holotype of *Actinocamax blackmorei* Crick, 1907); BMNH C44331 and C44254, East Harnham, top *pilula*-basal *quadrata* Zone; BGS GSM 101425, Mottisfont, top *pilula*-basal *quadrata* Zone; BMNH C44382, Micheldever, *coranguinum* Zone.

In addition to these specimens from southern England, three specimens from northern England and France are also included in the present study: (1) BMNH C46392, Ruston Parva, Yorkshire, *pilula* Zone (see Brighton 1930), (2) BMNH C10896, from flinty Chalk at Fimber, Yorkshire, *coranguinum* Zone (see Crick 1906); (3) BMNH C32498, Breteuil, France, probably top *pilula* Zone or base of *quadrata* Zone. According to I. Jarvis (in litt. 1986) this specimen most likely came from the large complex of abandoned phosphatic chalk quarries referred to as Hardivillers by Jarvis (1980).

Remarks. Specimens of the *B. grossouvrei* group are characterized by their large, ventrally flattened guards, which are lanceolate to strongly lanceolate in ventral view. Moreover, they generally have a shallow pseudoalveolus, the cross-section of which is triangular, and juvenile guards are long and elongated (Christensen 1986). About 100 specimens have been recorded from England, France, West Germany, Scania in southern Sweden, and the Russian Platform, and these specimens have been assigned to eleven species and subspecies (see Christensen 1986). The group has been the subject of excessive subdivision by earlier authors, and hopefully, the revision of this group by F. Schmid (Künzelsau) and M.-G. Schulz (Kiel) will help in solving these taxonomic problems. It should be stressed that only adult specimens have been figured previously; this may be due to the fact that juvenile and adolescent specimens are extremely rare.

Those English and French specimens of the *B. grossouvrei* group that have not been described or figured earlier, and the holotype of *A. blackmorei* are briefly commented upon below.

1. BMNH C42818. The holotype of *A. blackmorei* (Pl. 3, figs 1–4). The most anterior end of the guard is missing. It seems that the anterior end was ground, because it is completely flat and there is no trace of a shallow central pit for housing the phragmocone, or of a ventral furrow.
2. BGS GSM 101425 (Pl. 3, figs 5 and 6). An adult specimen which is strongly lanceolate in ventral view. The anterior part of the guard is badly preserved due to weathering, and the pseudoalveolus is not present.
3. BMNH C44331 (Pl. 3, figs 18–21). An adolescent specimen, which is only very slightly lanceolate in ventral view. The most anterior part of the guard is not preserved due to weathering, and only the most posterior part of the pseudoalveolus is present.
4. BMNH C44254 (Pl. 3, figs 10–13). A juvenile guard, which is strongly lanceolate in ventral and lateral views. The anterior end of the guard is flat with a pit in its centre and shows the concentric growth layers of the guard and radiating ribs. Moreover, the cross-section of the anterior end is subtriangular and a deep, short, ventral furrow is present. This specimen differs from other specimens of the *B. grossouvrei* group by having a flat anterior end. In the structure of the anterior end it resembles Turonian and early Coniacian species of *Actinocamax* (cf. Christensen 1982). The specimen is tentatively placed in the *B. grossouvrei* group due to its elongated guard which is strongly lanceolate in ventral view.
5. BMNH C44382 (Pl. 3, figs 14–17). A juvenile guard which is lanceolate in ventral view. The guard has anteriorly a shallow pseudoalveolus the cross-section of which is subtriangular. This specimen is somewhat similar to specimen no. A4331-1 (Ernst 1964*a*, Pl. 3, fig. 7) from the Lower Santonian of Kellermanshof near Essen, GFR. It was figured as *Gonioteuthis lundgreni/westfalica*.
6. BMNH C32498 (Pl. 3, figs 7–9). An adult specimen which is strongly lanceolate in ventral and lateral views. The guard has a shallow pseudoalveolus, the cross-section of which is subtriangular. A short ventral fissure is present.

Distribution. The stratigraphical range of the *B. grossouvrei* group was surveyed by Christensen (1986). *B.* ex gr. *grossouvrei* occurs in NW Germany and Scania in the basal Lower Campanian *G. granulataquadrata* Zone and the uppermost Lower Campanian *G. quadrata gracilis*/*B. mucronata* Zone or equivalent zones. In France and on the Russian Platform the group occurs in the Upper Santonian and Lower Campanian. The specimen from France commented upon above is probably from the top *pilula* Zone and/or base of the *quadrata* Zone. The two specimens from Fimber and Micheldever are from the Lower Santonian (possibly the latest Coniacian), whereas the remaining specimens are from the middle Lower Campanian (top *pilula* Zone and/or base of *quadrata* Zone). To sum up, the *grossouvrei* group occurs from the Lower Santonian (possibly the highest Coniacian) to the boundary between the Lower and Upper Campanian.

Genus BELEMNITELLA d'Orbigny, 1840

Type species. *Belemnites mucronatus* Schlotheim, 1813; ICZN Opinion 1328 (1985); name no. 2979.

Diagnosis. See Christensen (1975*a*).

Remarks. The International Commission on Zoological Nomenclature has designated under the plenary powers, specimen no. kca 5/2 in the collections of the Niedersächsisches Landesamt für Bodenforschung, Hannover, Germany, as neotype for *Belemnites mucronatus* Schlotheim (see ICZN 1985). The neotype was described and figured by Christensen *et al.* (1975, pl. 1, fig. 1).

Dozens of species and subspecies of *Belemnitella* from the Upper Campanian and Lower Maastrichtian have been established, and the majority of these taxa were erected on the basis of limited material by eastern European workers. The systematics of many of these taxa is in a state of disorder and they are poorly understood. Some of these taxa were discussed by Christensen (1986) and Christensen *in* Robaszynski and Christensen (1989).

Distribution. *Belemnitella* is widely distributed in the North European Province and has also been recorded from the northern part of the Tethyan Realm and the North American Province. The genus is known from the Lower Santonian to the uppermost Maastrichtian.

Belemnitella propinqua group

Remarks. Christensen (1986) included '*Actinocamax*' *lundgreni* Stolley from the Coniacian to Middle Santonian and *Belemnitella propinqua* (Moberg) from the Lower and Middle Santonian in

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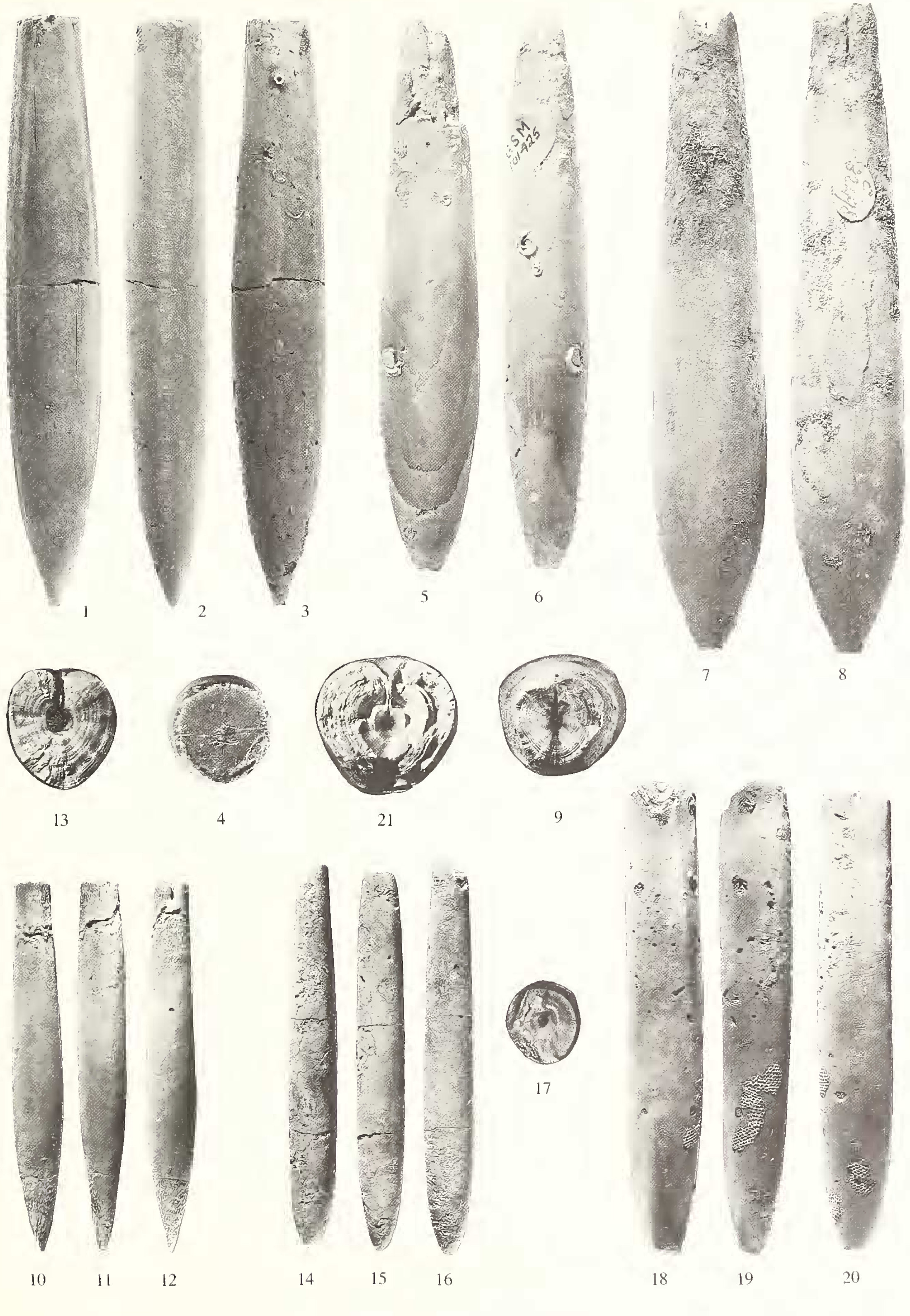
EXPLANATION OF PLATE 3

Figs 1–21. *Belemnellocamax* ex gr. *grossouvrei* (Janet) from England (1–6, 10–21) and France (7–9). 1–4, cast of holotype of *Actinocamax blackmorei* Crick, BMNH C10895 (plaster cast) and BMNH C42818, W. Harnham, top *pilula* Zone-basal *quadrata* Zone; 1, dorsal view; 2, lateral view; 3, ventral view; 4, view of the anterior end, ×1·5. 5–6, BGS GSM 101425, specimen from Mottisfont, locality no. 1067 of Brydone (1914), top *pilula* Zone-basal *quadrata* Zone; 5, ventral view; 6, lateral view. 7–9, BMNH C32498, specimen from Breteuil, France, probably top *pilula* Zone-base *quadrata* Zone; the specimen probably came from the large complex of abandoned phosphatic chalk quarries, referred to as Hardivillers by Jarvis (1980); 7, dorsal view; 8, ventral view; 9, view of the anterior end, ×1·5. 10–13, BMNH C44254, a juvenile specimen from East Harnham, top *pilula* Zone-basal *quadrata* Zone; note the flat anterior end with a pit in its centre, and the short, deep ventral furrow; 10, dorsal view; 11, lateral view; 12, ventral view; 13, view of the anterior end, ×3. 14–17, BMNH C44382, a juvenile specimen from Micheldever, *coranguinum* Zone; 14, dorsal view; 15, lateral view; 16, ventral view; 17, view of the anterior end, ×2. 18–21, BMNH C44331, a specimen from East Harnham, top *pilula* Zone-basal *quadrata* Zone; 18, dorsal view; 19, lateral view; 20, ventral view; 21, view of the anterior end, ×2.

All specimens are coated with ammonium chloride. All figures are natural size unless otherwise stated.



CHRISTENSEN, *Belemnellocamax*

the *Belemnitella propinqua* group. *B. propinqua* is generally considered to be the earliest representative of the genus *Belemnitella*. It is a well-defined species which was redescribed by Christensen (1971, 1973). It evolved from '*A.*' *lundgreni*.

'*A.*' *lundgreni* was placed in *Gonioteuthis* (*Goniocamax*) by Naidin (1964) together with several other species, including the earliest members of the *Gonioteuthis* lineage. This suggestion was criticized by Ernst and Schulz (1974) and Christensen (1982). Ernst and Schulz suggested that the subgenus *Goniocamax*, type species '*A.*' *lundgreni*, should be elevated to a genus or considered a subgenus of *Belemnitella*. They also suggested that only '*A.*' *lundgreni* and its ancestors should be assigned to *Goniocamax*. This suggestion must await further studies and is outside the scope of the present paper. '*A.*' *lundgreni*, however, is here placed in the *B. propinqua* group because it is closely allied to *B. propinqua*.

'*Actinocamax*' *lundgreni* Stolley, 1897

Plate 4, figs 1–6

1897 *Actinocamax lundgreni* Stolley, p. 285, pl. 3, figs 16–20 (*non* pl. 3, fig. 15).
1897 *Actinocamax mammillatus* mut. (ant.) *bornholmensis* Stolley, p. 288, pl. 4, fig. 1.
1897 *Actinocamax propinquus* Moberg mut. (var.) nov. Stolley, p. 295, pl. 3, fig. 23.
1912 *Actinocamax propinquus* Moberg; Arkhangelsky, p. 585, pl. 10, figs 14 and 15, ? *non* 23–27, 34–36.
1912 *Actinocamax intermedius* Arkhangelsky, p. 582, pl. 9, figs 30 and 31; pl. 10, fig. 6, 16–18, ? *non* 27.
1915 *Actinocamax plenus* Miller var. *excavata* Sinzow, p. 144, pl. 8, figs 14–17, ? *non* 18.
1918 *Actinocamax bornholmensis* Stolley; Ravn, p. 33, pl. 2, fig. 7.
1918 *Actinocamax* sp. (cfr. *Act. strehlenensis* Fritsch); Ravn, p. 34, pl. 2, fig. 8.
1946 *Actinocamax lundgreni* Stolley; Ravn, p. 30.
1949*a* *Belemnitella propinqua* (Moberg); Jeletzky, p. 416, text-figs 1 and 2 (*non* text-figs 3 and 4).
1957 *Actinocamax lundgreni lundgreni* Stolley; Birkelund, p. 13, pl. 1, figs 5 and 6.
1957 *Actinocamax lundgreni excavata* (Sinzow); Birkelund, p. 18, pl. 1, figs 7 and 8.
1957 *Actinocamax* aff. *westfalicus* (Schlüter); Birkelund, pp. 27–28, pl. 2, fig. 3.
1958 *Actinocamax intermedius* Arkhangelsky; Nikitin, p. 5, pl. 1, figs 4–8.
1958 *Actinocamax propinquus* Moberg; Nikitin, p. 12, pl. 1, figs 9–15; pl. 3, fig. 7.
1964*a* *Gonioteuthis lundgreni*/aff. *westfalica* sensu Birkelund; Ernst, p. 161, pl. 3, figs 5 and 6.
1964 *Gonioteuthis* (*Goniocamax*) *lundgreni lundgreni* (Stolley); Naidin, p. 127, pl. 7, figs 5–7.
1964 *Gonioteuthis* (*Goniocamax*) *lundgreni excavata* (Sinzow); Naidin, p. 133, pl. 7, fig. 8.
1972 *Actinocamax* (*Actinocamax*) *propinquus propinquus* Moberg; Glazunova, p. 106, pl. 45, figs 1–5.
1972 *Actinocamax* (*Actinocamax*) aff. *propinquus propinquus* Moberg; Glazunova, p. 107, pl. 46, fig. 1.
1972 *Gonioteuthis* (*Goniocamax*) cf. *lündgreni lündgreni* (Stolley); Glazunova, p. 113, pl. 46, figs 3 and 4.
1973 *Gonioteuthis lundgreni* (Stolley); Christensen, p. 131, pl. 10, figs 6–9.
1974 *Gonioteuthis* (*Goniocamax*) *lundgreni lundgreni* (Stolley); Naidin, p. 211, pl. 73, fig. 8.
1974 *Gonioteuthis* (*Goniocamax*) *lundgreni excavata* (Sinzow); Naidin, p. 211, pl. 73, fig. 9.
1975*a* *Actinocamax lundgreni* Stolley; Christensen, p. 28.
1982 *Actinocamax lundgreni* Stolley; Christensen, p. 76.
1986 '*Actinocamax*' *lundgreni* Stolley; Christensen, p. 30.

Lectotype. The specimen figured by Stolley (1897, pl. 3, fig. 18) was designated as lectotype by Birkelund (1957, p. 4).

Material. BMNH C44380, C44383, Micheldever, Hants, *coranguinum* Zone; BMNH C43506, Gravesend, Kent, *coranguinum* Zone.

Dimensions.

	L	D	DVDAE	LDAE	MLD	RQ	SQ
BMNH C44380	49*	4·7	5·6	4·7	7·2	10·4	8·8
BMNH C44383	53*	4·2	6·4	5·6	6·8	12·6	8·3
BMNH C43506	54*	5·2	7·8	—	8·9	10·4	6·9

(* estimated)

Short description. The length of the guard is up to 70 mm. The guard is stout and lanceolate in ventral view and slightly lanceolate, subcylindrical or high conical in lateral view. It is markedly flattened ventrally and the apex is acute. The Riedel Quotient varies from about 6 to about 12, and the cross-section of the anterior end is subtriangular. The walls of the pseudoalveolus are straight or convex and often have conellae. The surface of well-preserved guards has longitudinal striae and rather prominent vascular markings.

Remarks. Stolley (1897) distinguished three taxa from the Coniacian of Bornholm: *Actinocamax lundgreni* from the 'Glass marl' at Muleby, *A. mammillatus* mut. *bornholmensis* from the Arnager Limestone west of Arnager, and *A. propinquus* mut. (var.) nov. from the marl at Stampe Å (brooklet). Ravn (1946) placed *A. mammillatus* mut. *bornholmensis* in the synonymy of *A. lundgreni*, and this view was followed by later authors, including Birkelund (1957), Jeletzky (1958), Naidin (1964), and Christensen (1973). *A propinquus* mut. (var.) nov. is also considered a synonym of *A. lundgreni* (Christensen unpublished).

Affinity. The first member of the *Gonioteuthis* lineage, *G. westfalica praewestfalica* from the Middle and Upper Coniacian, and the first member of the *Belemnitella lineage*, '*A.*' *lundgreni* from the Lower Coniacian to Lower Santonian, are both characterized by having ventrally flattened guards which are lanceolate in ventral view. Moreover, both taxa have vascular markings and longitudinal striae. '*A.*' *lundgreni* differs, however, from *G. westfalica praewestfalica* by having a deeper pseudoalveolus and in being larger. In addition, '*A.*' *lundgreni* often has conellae on the walls of the pseudoalveolus.

Distribution. '*A.*' *lundgreni* occurs commonly on the Russian Platform, on Bornholm, Denmark, and in southern Sweden. Outside this area it is rare and has been recorded from NW Germany (Ernst 1964*a*; Christensen 1973, p. 133) and southern England (herein).

Christensen (1973) reviewed the biostratigraphical age of the species and concluded that it had its first occurrence in the late Coniacian and continued into the early Santonian. This was based on the assumption that the Arnager Limestone and 'Glass marl', stratum typica of '*A.*' *lundgreni* and *A. mammillatus* mut. *bornholmensis*, are of late Coniacian age. Recent studies of the inoceramid bivalve faunas of the Arnager Limestone Formation by K.-A. Tröger (Freiberg) have shown, however, that the Arnager Limestone west of Arnager is Lower Coniacian, the 'Glass marl' at Muleby is upper Lower Coniacian, and the marl at Stampe Å is lower Middle Coniacian in inoceramid terms. On ammonite evidence, however, the Arnager Limestone west of Arnager is at least Middle Coniacian (Kennedy and Christensen 1991). '*A.*' *lundgreni* also occurs together with *G. westfalica* and *Belemnitella propinqua* in parts of the Bavnodde Greensand Formation which is Lower Santonian (Christensen unpublished). It can thus be concluded that the stratigraphic range of '*A.*' *lundgreni* is Lower Coniacian to Lower Santonian.

'*Actinocamax*' ex gr. *lundgreni* Stolley, 1897

Plate 4, figs 7–12

1907 *Actinocamax* sp. Crick, p. 392, text-fig. 2.

Material. BMNH C10576, Fletcher and Co's Pit, Gravesend, Kent, *coranguinum* Zone; BMNH C59278, Grays, Essex, *coranguinum* Zone.

Short description. BMNH C10576 is a 70·6 mm long fragment, consisting of approximately the anterior two-thirds of the guard. It is estimated that the total length of the guard may have been 105–110 mm. It is lanceolate in ventral view and subcylindrical in lateral view. The guard has anteriorly a shallow pseudoalveolus 15 mm deep. The cross-section of the anterior end is subtriangular and the walls of the pseudoalveolus are covered by large, closely spaced conellae. Ventrally the guard is flattened and the surface of the guard is smooth.

BMNH C59278 is 54 mm long, but the most anterior part of the guard is not preserved. It is lanceolate in ventral view and slightly lanceolate in lateral view. The guard has anteriorly a shallow pseudoalveolus with walls covered by conellae. The depth of the preserved part of the pseudoalveolus is 6·8 mm and the cross-section of the alveolar end seems to have been subtriangular. Ventrally the guard is markedly flattened and the surface is smooth.

Remarks. BMNH C10576 was fully described by Crick (1907) who assigned it to *Actinocamax* sp., after having discussed its affinity to the *grossouvrei* group. Later on, it was assigned to the *Mammillata* group by Jeletzky (1949*b*), the *grossouvrei* group by Christensen (1975*a*), and possibly the '*A*.' *lundgreni* group by Christensen (1986). C10576 shares many characters with the *grossouvrei* group, including the size, shape and ventral flattening of the guard, the cross-section of the alveolar end, and the surface sculpture. It has, however, a deeper pseudoalveolus than the *grossouvrei* group, and it is estimated that the Riedel Quotient may have been about 7. In addition, it has many closely spaced conellae. C10576 resembles '*A*.' *lundgreni* in the shape and ventral flattening of the guard, and the depth of the pseudoalveolus. It is, however, larger than '*A*.' *lundgreni*. On the basis of the depth of the pseudoalveolus, it is tentatively referred to as '*A*.' ex gr. *lundgreni*.

BMNH C59278 also has characters in common with the *grossouvrei* group and '*A*.' *lundgreni*. On the basis of the depth of the pseudoalveolus (Riedel Quotient estimated to be about 5) it is tentatively referred to as '*A*.' ex gr. *lundgreni*.

Distribution. The specimens from Grays and Gravesend are considered to be from the Lower Santonian (see above).

Belemnitella propinqua propinqua (Moberg, 1885)

Plate 4, figs 13–18; Plate 5, figs 11–14

Synonymy. See Christensen (1971).

Holotype. By monotypy the specimen figured by Moberg (1885, pl. 5, fig. 25). It was refigured by Christensen (1971, pl. 1, fig. 1).

Material. BMNH C5502, Grays, Essex, *coranguinum* Zone; BMNH C43508 and C43519, Gravesend, Kent, *coranguinum* Zone.

EXPLANATION OF PLATE 4

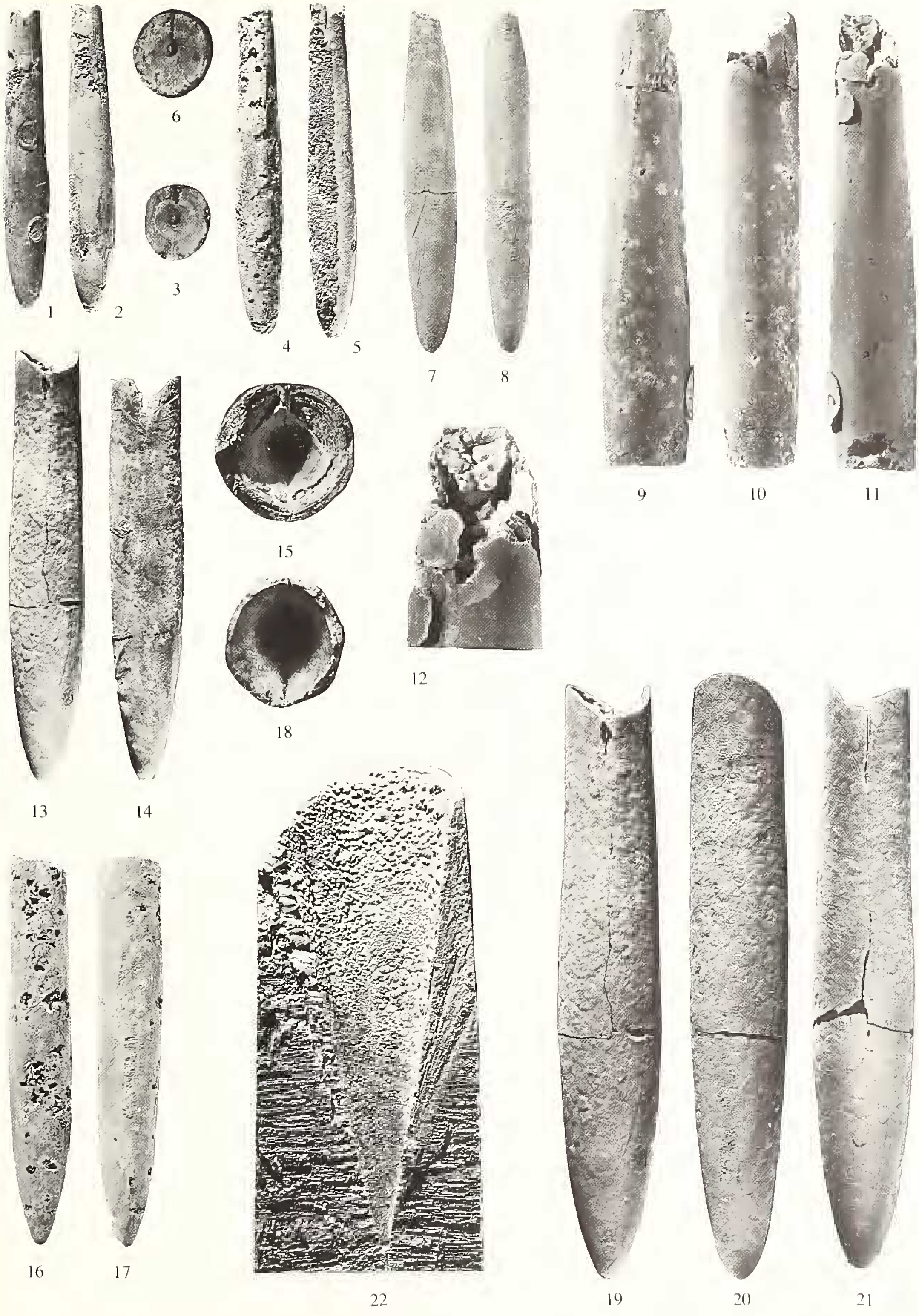
Figs 1–6, '*Actinocamax*' *lundgreni* Stolley. 1–3, BMNH C44380, Micheldever, *coranguinum* Zone; 1, dorsal view; 2, ventral view; 3, view of the anterior end, ×2. 4–6, BMNH C44383, Micheldever, *coranguinum* Zone; 4, dorsal view; 5, ventral view; 6, view of the anterior end, ×2.

Figs 7–12. '*Actinocamax*' ex gr. *lundgreni* Stolley. 7–8, BMNH C59278, Grays, *coranguinum* Zone; 7, dorsal view; 8, lateral view. 9–12, BMNH C10576, Fletcher and Co's Pit, Gravesend, *coranguinum* Zone; specimen figured as *Actinocamax* sp. by Crick (1907, text-fig. 2); 9, dorsal view; 10, lateral view; 11, ventral view; 12, view of the anterior end showing conellae, ×2.

Figs 13–18. *Belemnitella propinqua* (Moberg). 13–15, BMNH C43519, Gravesend, *coranguinum* Zone; 13, dorsal view; 14, ventral view; 15, view of the anterior end, ×2. 16–18, BMNH C5502, Grays, *coranguinum* Zone; 16, dorsal view; 17, lateral view; 18, view of the anterior end, ×2.

Figs 19–22. *Belemnitella* cf. *praecursor* Stolley, BMNH C43288, Porchester Pit, Hampshire; specimen labelled '*mucronata*' Zone, but according to Griffith and Brydone (1911) this pit is placed in the Subzone of *G. quadrata*; 19, dorsal view; 20, lateral view; 21, ventral view; 22, view of the split anterior end showing conellae, *c*. ×2·5.

All specimens are coated with ammonian chloride, except figs 9–12, and are natural size unless otherwise stated.



CHRISTENSEN, '*Actinocamax*', *Belemnitella*

Short description. A *Belemnitella* with a rather sturdy guard, lanceolate in ventral view and slightly lanceolate or subcylindrical in lateral view. The cross-section of the pseudoalveolus at the alveolar end is subtriangular to pointed oval. The walls of the pseudoalveolus are covered by closely spaced concellae. The Riedel Quotient varies from a little less than three to about four.

The most anterior part of the guard in C43508 and C43519 is not preserved. It is estimated that the Riedel Quotient is about 4 in C43508 and about 3 in C43519.

Dimensions.

	L	D	DVDAE	LDAE	MLD	LVF	RQ	SQ
BMNH C5502	60·5	19·6	10·0	8·9	10·2	6·0	3·1	6·1

Remarks. Christensen (1971, 1973) described the species in detail on the basis of Swedish and Danish material, including the holotype. Christensen (1971) listed synonyms and showed that the species had been misinterpreted by Russian palaeontologists. The following taxa were considered to be synonyms of *B. p. propinqua*: *Actinocamax propinquus*? Moberg, 1885, *Belemnitella mucronata* mut. *anterior* Stolley, 1897, *B.* ex gr. *mirabilis* Jeletzky, 1948, *A. propinquus ravni* Birkelund, 1957, *Gonioteuthis jeletzkyi* Kongiel, 1962, and *B. rylskiana* Nikitin, 1958.

Naidin (1974) employed a different concept of *B. p. propinqua* from that of Christensen (1971, 1973, 1986, and herein). He recognized *B. p. propinqua* from the Lower Santonian and *B. propinqua rylskiana* from the upper Lower to Upper Santonian, in addition to the dubious *B. propinqua mirabilis* Arkhangelsky, 1912 from the Santonian of northern Kazakhstan.

Distribution. *B. p. propinqua* occurs on the Russian Platform, on Bornholm, Denmark, and in southern Sweden. Outside this area it has only been recorded from southern England (herein). It occurs in the Lower and Middle Santonian.

Belemnitella praecursor group

Remarks. Christensen (1986) tentatively placed *B. alpha* Naidin and *B. praecursor* Stolley from the lower and middle Lower Campanian in this group. The two taxa were fully discussed, including their mutual relationship, and their relationship to *B. mucronata* (Schlotheim) from the uppermost Lower Campanian and Upper Campanian (see also Christensen 1975*a*; Christensen and Schmid 1987).

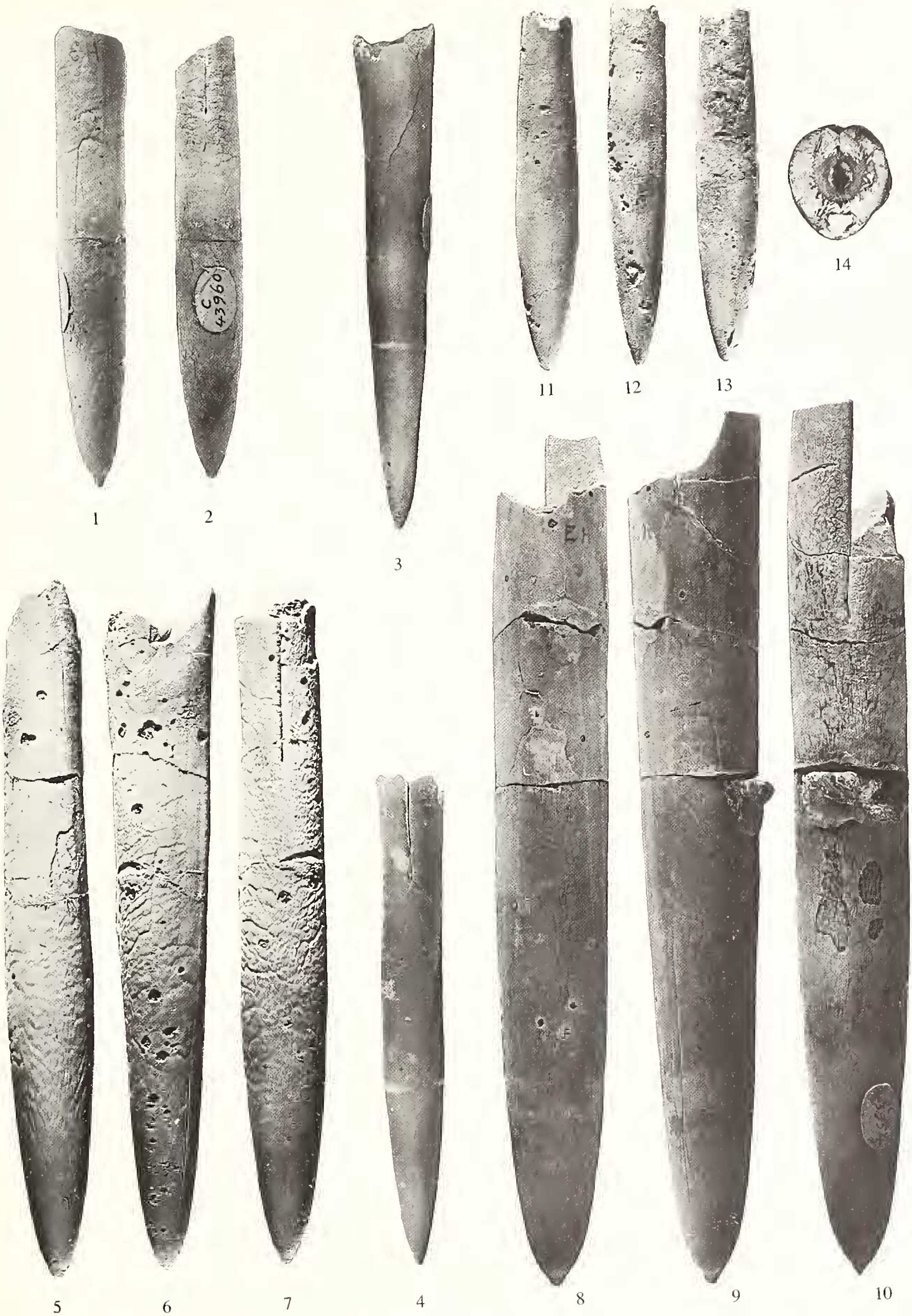
B. praecursor differs from *B. alpha* in several characters (see below), but it should be stressed that it is not possible on the basis of only a few specimens to assign them safely to either *B. praecursor* or *B. alpha* because the range of variation overlaps.

EXPLANATION OF PLATE 5

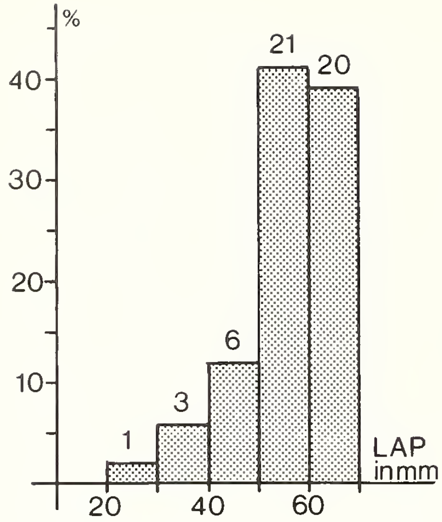
Figs 1–10. *Belemnitella praecursor* Stolley. 1–2, BMNH C43960, East Harnham, top *pilula* Zone-basal *quadrata* Zone; 1, lateral view; 2, ventral view. 3–4, BMNH C43964, East Harnham, top *pilula* Zone-basal *quadrata* Zone; a smooth and slender specimen; 3, lateral view; 4, ventral view. 5–7, BMNH C44149, East Harnham, top *pilula* Zone-basal *quadrata* Zone; specimen figured as *B. lanceolata* by Blackmore (1896, pl. 1, fig. 1); 5, dorsal view; 6, lateral view; 7, ventral view. 8–10, BMNH C43954, East Harnham, top *pilula* Zone-basal *quadrata* Zone; 8, dorsal view; 9, lateral view; 10, ventral view.

Figs 11–14. *Belemnitella propinqua* (Moberg), BMNH C43508, Gravesend, *coranguinum* Zone; 11, dorsal view; 12, lateral view; 13, ventral view; 14, view of the anterior end, ×2.

All specimens are coated with ammonium chloride, and are natural size unless otherwise stated.



CHRISTENSEN, *Belemnitella*



TEXT-FIG. 14. Histogram of the length from apex to the protoconch (LAP) of *Belemnitella praecursor* from East Harnham. The figures above the bars are the actual number of specimens.

Belemnitella praecursor Stolley, 1897

Plate 5, figs 1–10; Plate 6, figs 1–4, 8–10

Synonymy. See Christensen and Schmid (1987).

Holotype. By monotypy the original of Stolley (1897, pl. 3, fig. 24). A cast of the holotype was figured by Christensen (1986, pl. 3, fig. 4) and Christensen and Schmid (1987, pl. 3, figs 4 and 5).

Material. 82 specimens (BMNH C5776, C43953–67, C43972–80, C43986–44007, C44009–31, C44134, C44160–2, C44245, and C59152–8) from East Harnham, top *pilula* Zone-basal *quadrata* Zone.

Description. The guard is long, well-preserved guards ranging up to 150 mm. In ventral view the guard is generally lanceolate with a constriction at the base of the ventral fissure, and in lateral view it is high conical. The guard is flattened ventrally over its entire length. The apical angle is acute in both juvenile and adult specimens, and the mucro is only slightly delimited.

The guard is slender; the ratio of the length from apex to protoconch and the dorso-ventral diameter at the protoconch varies from about 3 to about 6, being 3·4–4·6 in most specimens, and the mean value is about 4.

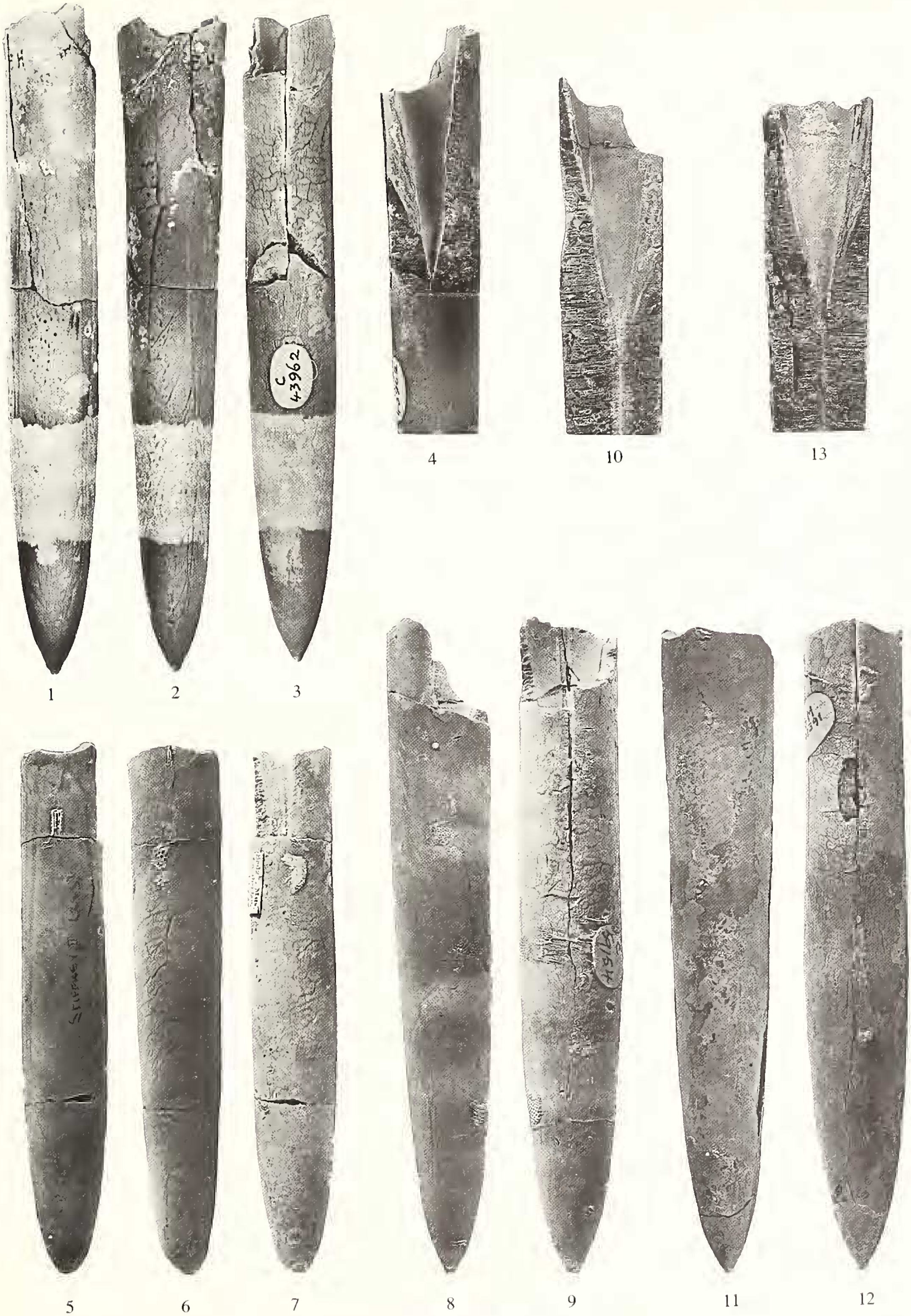
The depth of the alveolus is about half the length of the guard in well-preserved specimens. The shape of the bottom of the ventral fissure is generally straight or almost straight, but it may also be straight with an outward bend, S-shaped, curve, or undulating. The walls of the alveolus may be covered by conellae. The fissure angle and Schatzky distance are small, and the alveolar angle varies from 18–22° (see below).

EXPLANATION OF PLATE 6

Figs 1–4, 8–10. *Belemnitella praecursor* Stolley. 1–4, BMNH C43962, East Harnham, top *pilula* Zone-basal *quadrata* Zone; 1, dorsal view; 2, lateral view; 3, ventral view; 4, view of the anterior end showing internal characters. 8–10, BMNH C59154, East Harnham, top *pilula* Zone-basal *quadrata* Zone; 8, lateral view; 9, ventral view; 10, view of the split anterior end showing internal characters.

Figs 5–7, 11–13. *Belemnitella* cf. *praecursor* Stolley. 5–7, SM B97228, Stiffkey, *quadrata* Zone; 5, dorsal view; 6, lateral view; 7, ventral view. 11–13, BGS GSM 101391, Shawford, *quadrata* Zone; 11, lateral view; 12, ventral view; 13, view of the split anterior end showing internal characters.

All specimens are coated with ammonium chloride, and are natural size.



CHRISTENSEN, *Belemnitella*

Juvenile specimens are, by and large, smooth. Adolescent and adult specimens have weakly developed vascular markings, in addition to dorso-lateral depressions, dorso-lateral double furrows and longitudinal striae. The vascular markings are most prominent around the ventral fissure, and the longitudinal striae are typically more distinct than the vascular markings.

Biometry. A sample of *B. praecursor* from East Harnham was analysed by univariate and bivariate methods. Only very few specimens were split in the median plane, and thus the internal characters are known in fewer than ten specimens. The length from the apex to the protoconch was measured in unsplit specimens.

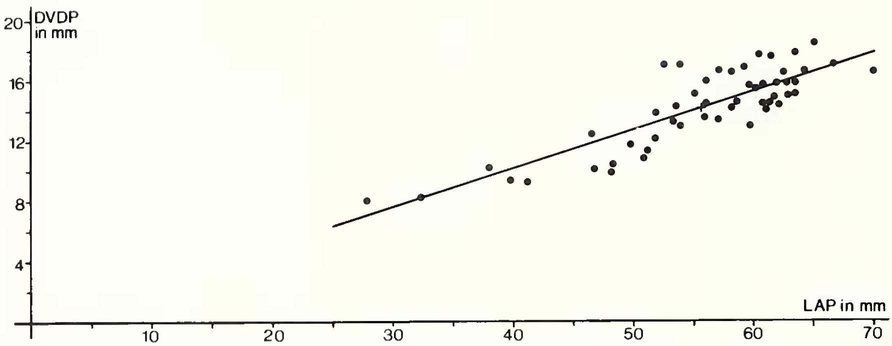
B. praecursor from East Harnham:

Character	*N*	$\bar{X}$	SD	CV	OR
LAP	51	55·6	8·6	15·5	27·8–69·9
DVDP	51	14·2	2·7	19·0	8·1–18·6
SD	8	8·2	1·9	22·8	6·4–11·3
FA	9	15·2	5·5	36·4	7·0–23·0
AA	8	20·2	0·6	2·9	19·5–21·5
LAP/DVDP	51	4·0	0·4	10·2	3·1–4·8

A histogram of the length from apex to protoconch is shown in Text-figure 14. It was tested for normality using the Kolmogorov–Smirnov-test for goodness of fit, and the test showed that the size-frequency distribution does not differ significantly from normality at the 5% level ($D = 0{\cdot}1361$; $0{\cdot}5 > P > 0{\cdot}2$ with 51 degrees of freedom).

Bivariate analysis. The scatter plot of the length from the apex to the protoconch vs the dorso-ventral diameter at the protoconch is shown in Text-figure 15, as is the regression line. The value of the correlation coefficient is very highly significant ($P < 0{\cdot}001$ with 49 degrees of freedom). A *t*-test on the *y*-intercept gave a value of 0·1289 with 49 degrees of freedom which is not significant ($0{\cdot}9 > P > 0{\cdot}8$), implying an isometric relationship of the variates.

On the basis of the univariate and bivariate analyses the sample from East Harnham can be regarded as homogeneous.



TEXT-FIG. 15. Scatter plot and regression line for *Belemnitella praecursor* from East Harnham. LAP = length from apex to the protoconch; DVDP = dorso-ventral diameter at the protoconch; + = mean value. $DVDP = -0{\cdot}1777 + 0{\cdot}2567\ LAP$; $N = 51$; $r = 0{\cdot}8347$; $SD_a = 1{\cdot}3782$; $SD_b = 0{\cdot}0239$; $SD_{yx} = 1{\cdot}4542$.

Remarks. *B. praecursor* was established on the basis of only one specimen and characterized as being smooth (Stolley 1897). Later Jeletzky (1955*a*) discussed the concept of *B. praecursor* and established two varieties, var. *media* and var. *mucronatiformis*, in addition to var. *praecursor*. He failed, unfortunately, to present appropriate biometrical data and/or a differential diagnosis for the three varieties.

Christensen and Schmid (1987) analysed the variation of the critical characters in a large sample of *B. praecursor* from the Vaals Formation (lower Lower Campanian, lower part of the *I. lingua/G. quadrata* Zone *sensu germanico*) of the C.P.L. Quarry at Hallembaye, Belgium. The results of the univariate and bivariate biometric analyses of the Hallembaye sample are reported below for comparison.

B. praecursor from Hallembaye (Christensen and Schmid 1987): *Univariate analysis.*

Character	N	$\bar{X}$	SD	CV	OR
LAP	46	60·9	11·8	19·4	20·1–79·2
DVDP	60	15·3	3·6	23·3	4·9–19·0
SD	57	6·4	1·3	20·9	4·2–10·2
FA	52	17·6	5·0	28·2	10·0–28·0
AA	59	20·1	0·9	4·3	18·0–22·0
LAP/DVDP	46	4·1	0·5	12·7	3·1–5·9

Bivariate analysis.

DVDP $= -2{\cdot}0831 + 0{\cdot}2854$ LAP; $N = 46$; $r = 0{\cdot}9208$; $SD_a = 0{\cdot}6684$; $SD_b = 0{\cdot}0108$; $SD_{yx} = 0{\cdot}8534$.

The relationship of the length from the apex to the protoconch *vs* the dorso-ventral diameter at the protoconch of this sample is very strongly allometric, and the juvenile and adolescent specimens are more slender than the adult specimens (Christensen and Schmid 1987).

The sample from East Harnham is closely similar to the sample from Hallenbaye with respect to slenderness and shape of the guard, surface sculpture, Schatzky distance and fissure angle. The East Harnham sample differs, however, from the Hallambaye sample in two ways: (1) the guard is generally slightly smaller, and (2) the relationship of the length from the apex to the protoconch *vs* the dorso-ventral diameter at the protoconch is isometric. Christensen (1986) and Christensen and Schmid (1987) considered the allometry to be diagnostic for the species. This assumption is now known to be incorrect.

The three varieties of *B. praecursor*, which '...are only morphologically varieties of the same specific type (parts of the same populations...' (Jeletzky 1955*a*, p. 482), must be treated as subspecies, following Article 45*g* of the International Code of Zoological Nomenclature (1985), because they have been used as subspecies in papers published before 1985. Christensen and Schmid (1987), however, did not recognize subspecies of *B. praecursor*, and subspecies are not recognized in the present paper. Extreme variants with a smooth guard, referred to as var. *praecursor* by Jeletzky, do occur in the East Harnham sample (see Pl. 5, figs 3 and 4).

Affinity. B. praecursor is closely allied to *B. alpha* Naidin from the lower and middle Lower Campanian, and *B. mucronata* (Schlotheim) from the uppermost Lower Campanian and Upper Campanian. The affinity was fully discussed by Christensen (1986) and Christensen and Schmid (1987). *B. praecursor* differs from *B. alpha* by being more slender, having a smaller Schatzky distance, and a larger fissure angle. Moreover, in *B. praecursor* the ratio of the length from the apex to the protoconch and the dorso-ventral diameter at the protoconch varies from about 3 to about 6, generally being 3·6–4·6, and the mean value is 4. In *B. alpha*, the ratio varies from about 3 to about 4, being 3·2–3·8 in most specimens, and the mean value is 3·5.

B. praecursor differs from *B. mucronata* by having weakly developed vascular markings, lacking a well-defined mucro, and being longer and more slender. The fissure angles of *B. mucronata* from the uppermost Lower Campanian and basal Upper Campanian and *B. praecursor* are very similar, whereas samples of *B. mucronata* from the middle Upper Campanian generally have larger fissure angles.

Distribution. B. praecursor has been recorded from Northern Ireland, through England, France, Belgium, northern Germany, Poland to Russia (Christensen 1986; Christensen and Schmid 1987).

The specimens from East Harnham are regarded to be from the middle Lower Campanian (see above). *B.*

praecursor occurs in West Germany in the lower Lower Campanian *G. granulataquadrata* Zone and the overlying *I. lingua/G. quadrata* Zone. A single specimen has also been collected in the middle Lower Campanian *Galeola senonensis* Zone. In Belgium, it occurs in the lower part of the *I. lingua/G. quadrata* Zone of the basal Lower Campanian. In Northern Ireland and southern England it occurs in the middle Lower Campanian. In Russia, *B. praecursor* appears in the uppermost Santonian and continues into the lower and middle Lower Campanian (Naidin and Kopaevich 1977; Naidin 1979, 1983). In the Corbières area of the French Pyrenees *B. praecursor* has recently been recorded from the uppermost Santonian (Christensen *et al.* 1991). Jeletzky (1955*b*) recorded a single specimen from the U.S.A. which probably came from the Niobrara Formation in Kansas.

Belemnitella cf. *praecursor*

Plate 4, figs 19–22; Plate 6, figs 5–7, 11–13

Material. BMNH C43288, Porchester Pit, Portsdown Hills, Hampshire; SM B97228–31, Stiffkey; BGS GSM 101370, 101376, 101379–81, Shawford.

Dimensions.

	LAP	DVDP	LDP	SD	FA	AA	LAP/DVDP
BMNH C43288	61·8	15·3	15·3	6·4	21·5	23·0	4·0
SM B97231	59·0	14·8	14·2	—	—	—	4·0
SM B97228	50·6	13·6	13·7	—	—	—	3·7
SM B97230	48·4	12·5	—	10·6	—	—	3·9
SM B97229	36·6	8·8	8·3	—	—	—	4·2
BGS GSM 101370	64·3	15·3	15·6	—	—	—	4·2
BGS GSM 101376	38·7	8·7	8·2	—	—	—	4·5
BGS GSM 101379	64·6	15·4	15·3	—	—	—	4·2
BGS GSM 101380	53·4	13·1	13·1	—	—	—	4·1
BGS GSM 101381	57·8	15·5	15·2	—	—	—	3·7

Remarks. The specimen from Porchester Pit is relatively slender (LAP/DVDP is 4·0), has weakly developed vascular imprints, and no well-defined mucro. The alveolus carries conellae (Pl. 4, figs 19–22) as in *B. praecursor* and *B. alpha*. The specimens from Stiffkey have weakly developed vascular imprints and the mucro is not well-defined. The mean value of the LAP/DVDP ratio of four specimens is 3·9, with an observed range from 3·7–4·2. The specimens from Porchester Pit and Stiffkey may be *B. praecursor* on the basis of their LAP/DVDP ratios, but they are referred to *B.* cf. *praecursor* owing to the small number of specimens.

I have also studied a small *Belemnitella* sample from Shawford, locality 1086 of Brydone (1912). Most of the specimens are unhorizoned, and the remaining specimens are from 'bottom course', 'lower course', '2nd course', and 'below upper marl layers' *sensu* Brydone. The *Belemnitella* fauna is heterogeneous in contrast to the *Belemnitella* sample from East Harnham (see above). It seems that specimens of *Belemnitella* from several horizons within the middle and upper Lower Campanian are present. Five specimens from the 'bottom course' and 'lower course' are referred to *B.* cf. *praecursor* on the shape and slenderness of the guard (the mean value of the LAP/DVDP ratios is 4·1 with an observed range of 3·7–4·5), and the weakly developed vascular markings. Some of the unhorizoned specimens may also be *B.* cf. *praecursor*. *B. mucronata*, however, is also present and this species appears in the uppermost Lower Campanian. The specimens of *B. mucronata*, however, may have come from another pit.

Distribution. The specimens from Stiffkey are regarded as coming from the upper Lower Campanian *papillosa* Zone (see above), and the specimens from Shawford from the middle Lower Campanian.

Belemnitella sp.

Material. SM B95274, Wells, *pilula* Zone; BMNH C44865, Sussex coast, base of *G. quadrata* Zone.

Remarks. SM B95274 is a fragment of a juvenile specimen consisting of the middle part of the guard. BMNH C44865 is a stout specimen (LAP: DVDP is 3·5) with vascular imprints. It was recorded as *Actinocamax mercyi* by Rowe (1900, p. 343). A specific determination of the two specimens is not possible.

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